COMPARING DENSITY ESTIMATES FROM A SHORT-TERM CAMERA TRAP SURVEY WITH A LONG-TERM TELEMETRY STUDY OF GIANT ARMADILLOS (Priodontes maximus)

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ABSTRACT. Population density is a key parameter in conservation, but remains a challenging metric to obtain for rare and cryptic species. We designed a camera trap array targeting the elusive giant armadillo (Priodontes maximus), estimated densities using spatially explicit capture-recapture models, and compared these with estimates from a previous eight-year telemetry study in the area. Density from the six-month camera trap survey (7.69 individuals/100km²) is nearly identical to that from the intensive telemetry study (7.65 ind./100 km²). We recommend the use of systematic camera trap arrays, which are much less expensive and time consuming, to obtain insights on the population status of elusive species across the Neotropics and inform conservation.

RESUMO. Comparando as estimativas de densidade de um levantamento de curto prazo de armadilhas fotográficas com um estudo de telemetria de tatu canastra (Priodontes maximus). A densidade de populações é um parâmetro chave em conservação e ecologia, mas é uma métrica difícil de se obter para espécies raras e de hábitos cripticos. Nós desenhamos uma matriz de armadilhas fotográficas para capturar o elusivo tatu canastra (Priodontes maximus), estimamos sua densidade usando modelos de captura e recaptura espacialmente explícitos, e comparamos essa estimativa com àquela obtida em um estudo anterior de oito anos de telemetria realizado na mesma área. A densidade obtida através do levantamento por armadilhas fotográficas com duração de seis meses (7.69 indivíduos/100km²) é praticamente idêntica àquela obtida no estudo intensivo de telemetria (7.65 ind./100 km²). Nós recomendamos o uso de matrizes sistematizadas de armadilhas fotográficas, que possuem um menor custo financeiro e em termos de mão de obra, ao longo da região Neotropical para obter conhecimento sobre o status populacional de espécies elusivas e informar medidas de conservação.

Key words: Cingulata, Pantanal, Priodontes maximus, spatially-explicit capture-recapture model.

Palavras-chaves: Cingulata, modelo de captura e recaptura espacialmente explícito, Pantanal, Priodontes maximus.
One of the key parameters in ecology and conservation biology is population density. Estimating population densities allows us to infer habitat suitability, evaluate the effects of species interactions, derive population matrix models to gauge long-term population viability, and helps to monitor the effectiveness of management and conservation actions (Royle et al. 2013, 2014; Hooker et al. 2020). There is a rich history of methods to estimate population densities including capture-recapture methods (Otis et al. 1978; Karanth & Nichols 1998), methods for unmarked individuals (e.g., distance sampling and N-mixture models, Buckland et al. 2004; Royle 2004), and more recently, spatially explicit capture-recapture models (Efford 2004; Royle et al. 2014). However, despite all of these advancements over the years, there remains consensus that reliable density estimates for elusive, rare, wide-ranging species that naturally occur at low densities are often difficult to obtain due to sampling and data limitations (Foster & Harmsen 2012).

The giant armadillo Priodontes maximus Kerr, 1792 (Mammalia: Cingulata) of South America is the largest living species of armadillo, with adults measuring up to 1.50 m and weighing up to 50 kg (Carter et al. 2016; Desbiez et al. 2019a). As nocturnal and fossorial animals with a natural rarity, they are quite cryptic across their broad distribution of habitats ranging from tropical forest to open savanna (Smith 2007; Abba & Superina 2010). The giant armadillos’ large size and myrmecophagous diet are traits that lead them to be solitary with extensive home ranges –median adult home-range area in the Pantanal is 2,518 ha– and little overlap between individuals of both sexes (Desbiez et al. 2020). As such, the species is currently classified as “Vulnerable” (A2cd), by the IUCN Red List of Threatened Species and the Brazilian Institute for Biodiversity Conservation (Anacleto et al. 2019; Chiarello et al. 2020) due mainly to habitat loss and hunting. Thus, monitoring their populations to learn more about this enigmatic species is essential to inform conservation actions.

Giant armadillos are difficult to capture and study in the wild (Eisenberg & Redford 1999; Silveira et al. 2009; Carter et al. 2016; Quiroga et al. 2017; Desbiez et al. 2020). However, the recent increase of studies using noninvasive camera trap sampling has provided important insights into the species ecology and natural history (Noss et al. 2004; Porfírio et al. 2012; Desbiez & Kluyber 2013; Aya-Cuero et al. 2017; Quiroga et al. 2017; Massocato & Desbiez 2017; Esteves et al. 2018; Desbiez et al. 2019b; Di Blanco et al. 2020). In many cases, individual armadillos can be identified from their unique scale and carapace patterns, which has allowed researchers to estimate their densities from camera trap arrays. Population density estimates from camera traps range from 1.27-5.55 individuals/100 km² in a protected area of the Brazilian Cerrado (Silveira et al. 2009), 5.77-6.28 ind./100 km² in the dry forests (Chaco and Chiquitano) of eastern lowland Bolivia (Noss et al. 2004), and 5.8 ind./100 km² on private lands in the Eastern Llanos of Colombia (Aya-Cuero et al. 2017). However, these studies were either originally designed and optimized to study large felids (e.g., jaguars Panthera onca and pumas Puma concolor; Noss et al. 2004; Silveira et al. 2009) or were more opportunistic without the use of a systematic grid (Aya-Cuero et al. 2017), which resulted in low (re)capture rates for armadillos that could bias density estimates.

Recently, Desbiez et al. (2020) reported the highest known density of P. maximus in private cattle ranches of the Brazilian Pantanal, with a median minimum density of 7.65 ind./100 km² (95% CI=5.68-10.19 ind./100 km². However, this estimate was derived from an eight-year telemetry study, which is too onerous, time-consuming, invasive, and logistically difficult to replicate throughout the species’ distribution. Therefore, the objectives of this study were to implement the use of a systematic camera trap array specifically designed for estimating densities of P. maximus and to compare to the long-term survey density calculated with telemetry in the same study area of Desbiez et al. (2020).

This study was carried out between July 2016 and January 2017 on private cattle ranches (19°16’60” S; 55°42’60” W) in the Brazilian Pantanal (Nhecolândia subregion) within the study area described by Desbiez et al. (2020). We established a camera trap array (n=75 camera sites) in an area where a cluster of 12 known individual P. maximus had been captured and monitored throughout an 8-year period (Fig. 1). All procedures followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2016).

To build the trap array, first we defined camera locations using ArcGIS, predefining their locations throughout the area occupied by the 12 animals and applying a 1 km spacing among them. Then, we applied a 250 m buffer around the pre-defined point locations to search for evidence of P. maximus to optimize the final placement of the camera traps (HC-500, HC-550, HC-600, and PC-850; Reconyx, Holmen, USA). Evidence included sleeping burrows, feeding excavations or even termite mounds with recent signs of predation as described in Massocato &
We avoided placing cameras at sites located in flooded areas or open grassland since giant armadillos avoid these areas. We set cameras traps to rapid fire mode, recording three to ten consecutive photos without any delays between triggers for 60-70 consecutive days, and cameras were active 24 hours a day. The survey area was approximately 14 000 ha with the rotation of 25 unpaired cameras across three consecutive periods.

Following Massocato & Desbiez (2019), individual *P. maximus* where identified using morphological characteristics that included: cephalic scale pattern, tail markings, light band width and shape above the base of tail, hind limbs, flank scale pattern, and natural marks. Once we reviewed all camera trap photos, we created detection matrices for each individual identified across all camera trap sites for each camera trap night. We used these observations to compute simple summary statistics including mean maximum distance moved (MMDM) and mean distance moved between consecutive captures for individuals captured across multiple sites to compare to other camera trap studies (Noss et al. 2004; Silver et al. 2004). We used these detection histories within a spatially explicit capture-recapture model that accounts for individual animal movement and baseline detection probability in the density estimation process by incorporating auxiliary data from camera trap locations (Borchers & Efford 2008; Royle et al. 2013). This model structure included two parameters of interest: a baseline daily detection rate ($g_0$) when the camera is placed at the individuals’ estimated activity center and a scaling parameter ($\sigma$) for the distance decay as the camera trap location is placed further away from the estimated individual activity center. We considered six a priori models to predict the density, detection, and movement of giant armadillos in our study area. These included a constant model, and covariate models including sex, behavioral response, latent 2- and 3-point mixtures to account for unobservable heterogeneity, and time-varying effects on detection. We did not include covariates on the scaling parameter because tracked armadillos of both sexes were known to exhibit the same mean daily displacement, 1 651 m versus 1 636 m for females and males, respectively (Desbiez et al. 2020). To ensure that our study area was sufficiently large to encompass the home ranges of individuals on the periphery of our trap array and reduce bias in the density estimates, we buffered the trap array by an arbitrarily large 20 km buffer. We implemented these models with the “count” detector function (e.g., Poisson point process of individual distributions and repeated captures possible) assuming half-normal detection decay in the R package “secr” (Efford 2011; R Core Team 2020). We evaluated relative model support based on each model’s Akaike Information Criterion corrected for small sample size (AICc) and Akaike weight ($\omega_i$) to determine the best approximating density models (Burnham & Anderson 2002).
Our sampling effort was 68 cameras with 4,334 camera trap nights (excluding seven original camera sites that malfunctioned). We obtained a total of 36 *P. maximus* nocturnal capture events and recorded 35 solitary animals and one female with her juvenile pup. Ten known animals that had been monitored through telemetry where captured in 21 events, while eight events captured four new animals that were individually identified by their markings. The remaining seven events were excluded from analyses because individuals could not be distinguished due to the distance from the camera, inadequate position or partial detection, or blurry images due to fast individual movement or fogged camera lens. Individuals were captured across multiple sites on 20 occasions with mean distance between consecutive captures of individuals registered as 2,200 m and the MMDM by individuals registered as 3,492 m.

The most supported model (\(\omega_i=0.81\)) suggested that density, detection, and movement were constant (Table 1). The estimated armadillo density was 7.69 ind./100 km\(^2\) (± 2.79 SE; Table 2). The baseline daily detection rate was very low (\(g_0=0.002±0.001\) SE), and movement was relatively high (\(\sigma=2,360\) m±494 SE; Table 2). The model accounting for sex-specific detection received some additional model support (\(\omega_i=0.17\)), with a slight negative association with male armadillo detection compared to female detection (\(\beta=-0.006±0.012\) SE), resulting in a higher density estimate of 8.20 individuals/100 km\(^2\) (± 3.22 SE; Table 1).

We believe this is the first application of spatially explicit capture-recapture models to giant armadillo data. Our results suggest that spatially explicit capture-recapture models are effective and robust when applied to giant armadillo camera trap data from systematic trap arrays. The density estimates encountered here are nearly identical to those previously estimated based on long-term monitoring and home range (AKDE sensu Fleming et al. 2015) overlap patterns of known resident individuals (7.65 ind./100 km\(^2\) [95% CI=5.68-10.19 ind./100 km\(^2\)]) and when accounting for known residents and transient individuals (7.68 ind./100 km\(^2\) [95% CI=5.7-10.27 ind./100 km\(^2\)]: Desbiez et al. 2020). The current study was conducted over a short six-month period, with a noninvasive technique and experienced few logistical constraints. This contrasts to the previous eight-year invasive study (Desbiez et al. 2020) that required over 1,000 days in the field, with a minimum team of three people including a veterinarian which required specialized equipment, expertise and included extensive arduous fieldwork for capture and tracking of individuals. These results are therefore encouraging considering the financial and logistical aspects of camera traps compared to previous more intensive telemetry and long-term tracking methods.

The systematic camera trap array was effective at detecting all of the known individuals that occurred in the study area since 2011. From the 12 individuals monitored in the area, 10 are resident and two have occupied the area for a period and had died (subadult male, preyed-upon by puma) or dispersed (subadult male). The cameras further enabled us to register four additional animals, three adults (two males, one female) and a younger animal that had not been captured in this area during the past seven years. These animals could be transient, males performing exploratory behavior (Desbiez et al. 2020), or resident animals not previously captured.

Overall, the success rate at individual identification of *P. maximus* was 80% and only 7 detections could not be individually identified. This is because cameras where carefully placed at features in which animals pause to seek olfactory cues, which increases the chances that photographs will capture details of scale patterns (Massocato & Desbiez 2019). Similar to other taxa-specific studies (Wearn et al. 2013), camera trap placement strategy is one of the challenges of giant armadillo studies. Camera trap arrays developed for the study of big cats often place camera traps on trails (Silveira et al. 2009; Quiroga et al. 2017) leading to blurry images of armadillos during

### Table 1

Model selection statistics for spatially-explicit capture-recapture analyses of capture data from 14 individual giant armadillos (*Priodontes maximus*) using camera traps at the Baía das Pedras Ranch, Pantanal wetland, Brazil, from July 2016 until February 2017. Density and movement parameters were constant, but detection (\(g_0\)) was modeled as constant or variable dependent on sex, 2- or 3-point mixture processes, behavioral response, or time dependence. Included are AICc values (AICc), information distance from the top ranked model (ΔAICc), Akaike weight (\(\omega\)), number of parameters (\(K\)), and model log-likelihood (LogLik).

| Model | AICc | ΔAICc | \(\omega\) | K | LogLik |
|-------|------|-------|----------|---|--------|
| \(g_0()\) | 194.30 | 0.00 | 0.81 | 2 | -94.60 |
| \(g_0(\text{sex})\) | 197.40 | 3.10 | 0.17 | 3 | -94.50 |
| \(g_0(\text{h2})\) | 201.65 | 7.35 | 0.02 | 4 | -94.60 |
| \(g_0(\text{h3})\) | 213.21 | 18.91 | 0.00 | 6 | -94.60 |
| \(g_0(\text{behavior})\) | 437.00 | 242.70 | 0.00 | 3 | -214.30 |
| \(g_0(\text{time})\) | 437.04 | 242.74 | 0.00 | 3 | -214.32 |
displacement hindering the visualization of the fine scale patterns and making individual identification much more difficult.

Giant armadillos are naturally rare and occur at low densities (Abba & Superina 2010), but the robustness of our spatially explicit capture-recapture model density estimates, even with fairly limited number of detections, provides support for a call to scale these methods up across giant armadillos’ range and in different biomes. While the expansion of systematic camera trap arrays from across the Neotropics (e.g., Rovero & Ahumada 2017) may provide some insights with by-catch data, species-specific surveys with standardized arrays (~1 km-spacing) with high spatial coverage of study areas are vastly important to obtain the required individually identifiable data for giant armadillo population estimation and ecological inference. Furthermore, we recommend integration of these species-specific survey data with opportunistic by-catch data into range-wide integrated species distribution models (ISDMs – Schank et al. 2019) to further inform and promote the conservation of giant armadillos across their entire range. Camera traps have proven to be largely effective for monitoring a variety of threatened and endangered species (e.g., Karanth & Nichols 1998), and we provide evidence that short-term species-specific surveys paired with spatially explicit capture-recapture analyses provide robust density estimates for rare, wide-ranging nocturnal species with fossorial habits.

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Table 2

| Parameter | Estimate | SE       | LCI-UCI    |
|-----------|----------|----------|------------|
| Density   | 7.688    | 2.788    | 3.860–15.310 |
| g0        | 0.002    | 0.001    | 0.001-0.005 |
| σ         | 2360.206 | 493.952  | 1572.9-3541.5 |

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