

Unmanned aerial vehicle surveys reveal unexpectedly high density of a threatened deer in a plantation forestry landscape

JAVIER A. PEREIRA, DIEGO VARELA, LEONARDO J. SCARPA, ANTONIO E. FRUTOS
NATALIA G. FRACASSI, BERNARDO V. LARTIGAU and CARLOS I. PIÑA

Abstract The Vulnerable marsh deer *Blastocerus dichotomus*, the largest native cervid in South America, is declining throughout its range as a result of the conversion of wetlands and overhunting. Estimated densities in open wetlands of several types are 0.1–6.8 individuals per km². We undertook the first unmanned aerial vehicle (UAV) survey of the marsh deer to estimate the density of this species in a 113.6 km² area under forestry management in the lower delta of the Paraná River, Argentina. During 6–8 August 2019, at a time of year when canopy cover is minimal, we surveyed marsh deer using Phantom 4 Pro UAVs along 94 transects totalling 127.8 km and 8.6 km² (8.1% of the study area). The 5,506 photographs obtained were manually checked by us and by a group of 39 trained volunteers, following a standardized protocol. We detected a total of 58 marsh deer, giving an estimated density of 6.90 individuals per km² (95% CI 5.26–8.54), which extrapolates to 559–908 individuals in our 113.6 km² study area. As it has generally been assumed that marsh deer prefer open habitats, this relatively high estimate of density within a forestry plantation matrix is unexpected. We discuss the advantages of using UAVs to survey marsh deer and other related ungulates.

Keywords Argentina, *Blastocerus dichotomus*, drone, marsh deer, Paraná River Delta, population density, UAV, wetland

Introduction

The marsh deer *Blastocerus dichotomus*, the largest native cervid in South America, occurs from central Brazil to central Argentina (Pinder & Grosse, 1991). The species is declining throughout its range, mainly as a result of the conversion of wetlands and overhunting, and is categorized as Vulnerable on the IUCN Red List (Duarte et al., 2016). The primary habitat of this species is wetlands of several types and with different hydrological regimes (e.g. flooded grasslands, vegetated lagoons, swamps with floating marshes), with transitional areas between open water and terrestrial uplands used at finer scales (Tomas & Salis, 2000; Piovezan et al., 2010). Although the marsh deer is mostly associated with open habitats, the occasional use of forested areas by this ungulate has been reported (Pinder, 1996; Piovezan, 2004).

Marsh deer densities have been estimated in various types of open habitats, including the Pantanal of Brazil and the Iberá marshes of Argentina (Beccaceci, 1994; Mauro et al., 1995; Mourão et al., 2000; Tomas et al., 2001; Ávila, 2017), open, wet savannahs in Bolivia (Ayala-Crespo, 2010; Ríos-Uzeda & Mourão, 2012), the floodplains of the Paraná River (Mourão & Campos, 1995; Pinder, 1996; Andriolo et al., 2005, 2013; Tiepolo et al., 2010; Pereira, 2016) and other small wetlands (Peres et al., 2017). Estimated densities are 0.1–6.8 individuals per km² (Table 1). Although these densities were estimated for areas with various levels of anthropogenic disturbance (e.g. from almost pristine savannahs in Bolivia to wetlands artificially flooded during dam construction along the Paraná River), the highest marsh deer densities have generally been observed in landscape gradients, including transitional areas between open water and terrestrial uplands (Piovezan et al., 2010).

Aerial surveys are particularly useful for surveying large mammals, especially over large, open areas, because of the potential for high detection rates (Sinclair, 1972; Caughley & Grigg, 1981; Jachmann, 2001) and because the resulting estimates are more reliable than those from ground-based techniques (Guo et al., 2018). Aerial surveys using manned airplanes or helicopters have been the most common method employed for counting marsh deer (Table 1). However, aerial surveys using manned aircraft can be logistically difficult to implement, costly and pose a risk for operators, and are also potentially susceptible to biases related to the

JAVIER A. PEREIRA (ORCID orcid.org/0000-0002-0346-739X) Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”—Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

DIEGO VARELA (ORCID orcid.org/0000-0003-3123-6756) Instituto de Biología Subtropical, Universidad Nacional de Misiones—Consejo Nacional de Investigaciones Científicas y Técnicas, Asociación Civil Centro de Investigaciones del Bosque Atlántico, Misiones, Argentina

LEONARDO J. SCARPA (ORCID orcid.org/0000-0002-6655-9937), ANTONIO E. FRUTOS (ORCID orcid.org/0000-0001-5500-3637) and CARLOS I. PIÑA (Corresponding author, ORCID orcid.org/0000-0002-6706-5138, cidcarlos@infoaire.com.ar) Centro de Investigación Científica y de Transferencia Tecnológica a la Producción—Consejo Nacional de Investigaciones Científicas y Técnicas, Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Diamante, Entre Ríos, Argentina

NATALIA G. FRACASSI (ORCID orcid.org/0000-0003-0350-1858) Estación Experimental Agropecuaria Delta del Paraná, Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina

BERNARDO V. LARTIGAU Asociación para la Conservación y el Estudio de la Naturaleza, Buenos Aires, Argentina

Received 15 January 2021. Revision requested 1 April 2021.

Accepted 30 July 2021. First published online 8 June 2022.

This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

Oryx, 2023, 57(1), 89–97 © The Author(s), 2022. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605321001058

<https://doi.org/10.1017/S0030605321001058> Published online by Cambridge University Press

TABLE 1 Reported densities of the marsh deer *Blastocerus dichotomus*, by location, with habitat type, survey method and source.

Location (by country)	Density (individuals/km ²)	Habitat type	Method	Source
Argentina				
Paraná River Delta	6.90 (CI 5.26–8.54)	Forestry plantations, marshlands	Aerial counts (drones)	This study
San Alonso, Iberá	6.80	Temporarily flooded & well-drained grasslands	Aerial counts (airplane)	Ávila (2017)
Bolivia				
Llanos de Moxos	0.41	Open, wet savannah	Aerial counts (airplane)	Ríos-Uzeda & Mourão (2012)
Pampas de Heath, Madidi National Park	3.70	Humid savannah	Ground survey	Ayala-Crespo (2010)
Brazil				
Paraná River, area of Porto Primavera dam	1.90	Marshes, grasslands	Aerial counts (airplane)	Andriolo et al. (2013)
Paraná River, downstream of Porto Primavera dam	2.25	Marshes, grasslands	Aerial counts (helicopter)	Pinder (1996)
Ilha Grande National Park	1.50	Marshlands, degraded riverine forest	Aerial counts (airplane)	Tiepolo et al. (2010)
Capão da Cruz	0.98	Marshlands, riparian forest, plantations	Camera trapping	Peres et al. (2017)
Capão da Cruz	1.06	Marshlands, riparian forest, plantations	Aerial counts (helicopter)	Peres et al. (2017)
Pantanal	1.85	Flooded, open grasslands, savannah, forest patches	Aerial counts (airplane)	Tomas et al. (2001)

physiological and psychological limitations of human perception and potential reactions of the target species to the survey vehicle (Caughley, 1974; Bartmann et al., 1986; Beasom et al., 1986; Samuel et al., 1987; Fleming & Tracey, 2008). Unmanned aerial vehicles (UAVs or drones) present a new opportunity for surveying wildlife as the logistics of deploying them are less complex and the cost is lower than for manned aircraft, they can fly safely at low altitudes and they are particularly useful for surveying sensitive species (Chabot & Bird, 2015; Hodgson et al., 2018; Wang et al., 2019). However, there are also drawbacks of using UAVs, including reduced flight time, short operating distances, weather restrictions (most UAVs cannot fly in rain or moderately high winds), the potential for behavioural responses of animals to the UAVs, and the social concerns of using UAVs, including privacy, psychological responses and safety (Sandbrook, 2015; Hodgson & Koh, 2016; Wang et al., 2019). The use of UAVs for surveying a range of organisms (e.g. rare primates, de Melo, 2021; dolphins, Oliveira-da-Costa et al., 2020; caimans, Scarpa & Piña, 2019), and for other conservation uses (e.g. as a tool to mitigate negative interactions between people and wildlife; Hahn et al., 2017), continues to develop. Unmanned aerial vehicles have been employed to survey several large herbivores, including the elephant *Loxodonta africana* (Vermeulen et al., 2013), common hippopotamus *Hippopotamus amphibius* (Linchant et al., 2018), white-tailed deer *Odocoileus virginianus* (Preston et al., 2021), Tibetan antelope *Pantholops hodgsonii* (Hu

et al., 2020), Tibetan gazelle *Procapra picticaudata*, kiang *Equus kiang*, and blue sheep *Pseudois nayaur* (Guo et al., 2018), but to our knowledge they have not been used to survey the marsh deer.

The southernmost population of the marsh deer inhabits the lower delta of the Paraná River, Argentina (Varela, 2003; D'Alessio et al., 2006). This population, c. 500 km from the nearest population of the species (Pereira et al., 2019), is genetically distinct from other marsh deer populations (Márquez et al., 2006), suggesting it should be considered a separate management unit. This delta has been subjected to large-scale transformation since the mid 19th century (Galafassi, 2005; Baigún et al., 2008; Sica et al., 2016). The gallery forest that originally occupied the levees of islands has been almost entirely replaced by commercial plantations of poplar *Populus* sp. and willow *Salix* sp., and freshwater marshes have been drained to accommodate plantations and cattle pasture. Habitat conversion has been facilitated by embankments to protect tree plantations and cattle from recurrent floods, turning embanked areas into flood-free lands (Galafassi, 2005; Baigún et al., 2008; Quintana et al., 2014; Minotti, 2019).

These extensive habitat disturbances, together with poaching and predation by dogs, led to categorization of the marsh deer population of the Paraná Delta as Endangered (Pereira et al., 2019). However, most of this population (distributed across c. 2,700 km²) is associated with landscapes under forestry production (Varela, 2003;

Fracassi & Somma, 2010; Iezzi et al., 2018), and there is a need for an assessment of the interactions between the marsh deer and regional forestry practices. There has been no rigorous estimate of marsh deer density in this region, but an informed guess (Lartigau et al., 2012) suggested a population of c. 500 individuals over an area of 950 km² (c. 0.53 individuals/km²). The absence of a survey of marsh deer in this area precludes any attempt to assess the impact of human activities on this population or to evaluate the effectiveness of any management interventions to improve its status. Here we describe a UAV-based survey employed to estimate density of the marsh deer in an area under forestry management in the lower delta of the Paraná River. We contextualize our results with those of previous surveys of the species elsewhere, and discuss procedures to minimize sampling errors and biases.

Study area

This study was conducted in El Oasis property of the forestry company Arauco Argentina S.A. in the province of Buenos Aires, Argentina (Fig. 1), c. 19 km north of the city of Campana. This property is mostly surrounded by lands dedicated to forestry, silvopastoral systems and extensive cattle production. The landscape of El Oasis is mostly flat, with c. 87% of its 113.6 km² occupied by willow (69% of the land area in production), eucalyptus *Eucalyptus* sp. (17%), poplar (13%), pines *Pinus* sp. and ash *Fraxinus* sp. plantations of varying age, density and management practices (D. Artero, pers. comm., 2020). Some patches of native vegetation (freshwater marshes dominated by macrophytes such as *Scirpus giganteus* and the tree *Erythrina cristagalli*, and gallery forests of *Myrceugenia glaucescens* and *Blepharocalix salicifolia*), totalling 7.5 km², are maintained as a protected area. An extensive network of unmade roads provides access, and the property is almost completely enclosed by a perimeter embankment as a defence against floods. El Oasis was first certified under the Forest Stewardship Council (FSC) standard in 2014, and in 2019 was awarded an FSC ecosystems services certificate for demonstrating its positive impact in the conservation of the marsh deer.

Methods

We surveyed marsh deer using two Phantom 4 Pro UAVs (SZ DJI Technology Co., Shenzhen, China), each equipped with a high-definition camera (1" CMOS, 20 MP sensor; field of view 84°, 8.8/24 mm, f/2.8–f/11 auto focus at 1 m–∞) mounted on its 3-axis gimbal, transmitting a live-feed to the tablet-mounted remote control. A flight plan (i.e. a sequence of locations to be visited by the UAV, and flight parameters such as altitude and speed) was uploaded to

each device. Once the UAV was launched, it flew the pre-programmed path from the flight starting point, with an operator on the ground observing remotely.

An initial exploratory survey was conducted during 16–17 May 2019, during which six flight plans were flown (totalling 19.5 km). These flights were designed to test different flight parameters (i.e. speed, altitude) and image-collection schedules to maximize the probability of distinguishing a marsh deer from its surroundings in the various habitat types within the study area. After these initial flights, the following parameters were used for the surveys: altitude of 45 m above ground level (resulting in a 67.5 m wide transect), ground speed of 6.5 m/s, and a photograph taken every 5 s (resulting in a frontal overlap of c. 33% between consecutive photographs). Marsh deer did not noticeably react (i.e. escape behaviour was never observed) to the advance of a UAV at this combination of flight altitude and speed.

Survey flights were performed during 6–8 August 2019, in the austral winter, when leaf cover is lowest (poplar and willow are deciduous; Plate 1). A grid with cells of 1,500 m (north–south) × 100 m (east–west) was superimposed on an image of the study area, and transects of 1,500 m were defined by the intersection of north–south with east–west lines. As the perimeter of the study area is irregular and the length of the resulting transects at the property edges varied considerably, only transects > 760 m long were used. Transects were numbered and randomly selected to be included in the survey until 10% coverage of the study area was achieved. These transects (Fig. 1a) were transformed into flight paths in *DJI GS Pro* (Dà-Jiāng Innovations, Shenzhen, China). Each flight path was designed to encompass the greatest possible number of chosen transects, considering flight range constraints imposed by battery capacity. Once these flight paths were defined, additional transects were included; where the end and start positions of transects were greater than 1,500 m apart, we delineated additional east–west transects to be surveyed. The first and last 100 m of these transects were truncated (i.e. the photographs discarded) to avoid possible double counting of individuals. Flight paths < 500 m apart were flown consecutively within a short period of time (i.e. < 3 h), to minimize double counting as deer could have moved between adjacent transects (marsh deer did not react to the advance of the UAV and the species usually moves slowly). A one-way ANOVA was used to test if transect length affected the probability of recording a marsh deer, grouping transect lengths into four categories (760–1,040 m, 1,041–1,350 m, 1,351–1,640 m, > 1,640 m), with deer density on the transects (as individuals/ha) as the response variable.

The 5,506 photographs obtained from the surveys were manually checked by the authors and by 39 trained volunteers (training involved practice identifying deer and other species from photographs obtained during the exploratory survey). Each observer analysed a subset of images,

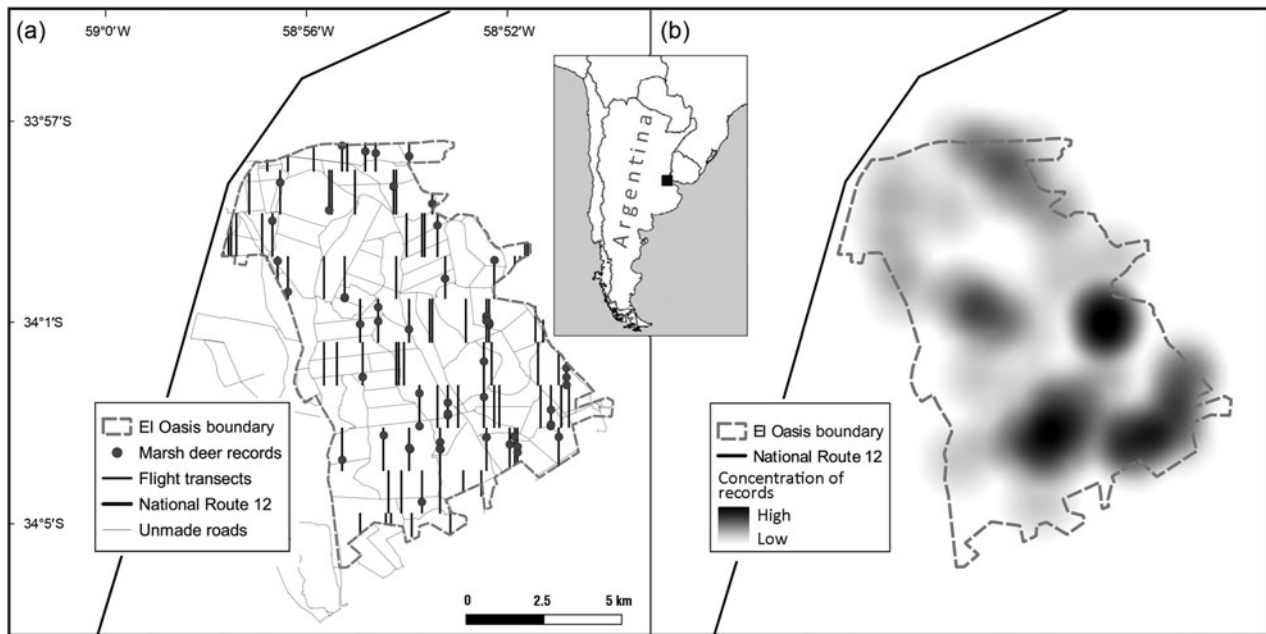


FIG. 1 (a) The locations of transects surveyed, using UAVs, for the marsh deer *Blastocerus dichotomus* within the plantation forestry landscape of El Oasis property, in the lower delta of the Paraná River, Argentina, during 6–8 August 2019, and the marsh deer records obtained. (b) A heatmap of these records, with a scale from high (black) to low (white) concentration of records.



PLATE 1 Examples of records of the marsh deer *Blastocerus dichotomus* in different habitat types from photographs taken during UAV flights at an altitude of 45 m above ground level within the El Oasis property in the lower delta of the Paraná River, Argentina (Fig. 1), during 6–8 August 2019.

following a standardized protocol: zooming in digitally on the image and looking from left to right and from top to bottom for marsh deer. Overlapping sequential images were compared to avoid double counting. Each photograph was checked by at least two independent observers. The total number of marsh deer recorded by all observers, excluding multiple detections of the same individual by more than one observer, was used to estimate marsh deer density.

We evaluated whether the ability of observers to detect deer was affected by them occurring in the centre of a

photograph compared to those occurring towards the borders of a photograph. For every photograph in which a marsh deer was detected, a grid of nine equal quadrants was superimposed digitally, allowing assignment of detection to only one of nine possible positions within the image (none of the photographs used to evaluate observers' ability to detect deer contained more than one deer). Thirty groups of 30 photographs each were assembled (i.e. 900 in total), with each group comprising 21 photographs without marsh deer and nine with a single deer in each of the nine

positions (photographs did not include the grid). Photographs assigned to each group were randomly selected from a subset of photographs featuring the same situation (i.e. with a deer in the top-right position, with a deer in the centre-left position, without a deer, etc.). Thirty volunteers (of the 39 who analysed the photographs) were each given a group of photographs for evaluation, but were not informed that the images had already been analysed. The probability of detecting a marsh deer in each of the nine positions within the photographs was estimated as the number of times observers detected a deer in each position divided by the total number of photographs (30) featuring the animal in this position. A χ^2 test was used to examine whether a deer had the same chance of being observed irrespective of its location in the photographs.

Marsh deer records obtained during flights were digitized using *Google Earth* (Google, Mountain View, USA) and converted to a GIS shapefile. A heatmap was used to visualize spatial patterns of marsh deer records, using *QGIS 3.12.2* (QGIS Development Team, 2020), to evaluate whether records were evenly distributed within the study area or circumscribed to a particular sector, which would preclude extrapolation of any density estimate to the whole study area.

Results

We surveyed 94 transects from 29 flight plans. Mean transect length was 1,359 m, totalling 127.8 km and 8.6 km² surveyed (8.1% of the 113.6 km² study area). Length of transect did not affect the probability of detecting a marsh deer (ANOVA $F_{3,90} = 0.24$, $P = 0.8$). Marsh deer were observed on 39 transects (41.5%), and the maximum number of individuals sighted on a single transect was three.

Fifty-eight marsh deer were detected and there were no significant differences in the probability of detecting a deer in each of the nine quadrants of a photograph ($\chi^2 = 0.74$, $df = 4$, $P = 0.947$). The heatmap showed that, although some records were clustered, marsh deer were widely distributed throughout the area surveyed (Fig. 1b). The estimated density of marsh deer was 6.90 individuals/km² (95% CI 5.26–8.54 individuals/km²), giving an estimated total abundance of 559–908 individuals in the 113.6 km² study area.

Discussion

Our estimate of the density of marsh deer is one of the highest recorded for the species (Table 1). Even in relatively well-conserved areas such as the savannahs of the Madidi National Park in Bolivia and the Pantanal wetlands of Brazil, estimated marsh deer densities were considerably lower than our estimate (except for one site in the Iberá wetlands, Argentina; Table 1). However, most of these previous

density estimates were obtained over large landscapes, using fixed-wing aircraft with line transects and distance sampling, and thus direct comparisons may be inappropriate.

As open habitats are generally considered to be preferred by marsh deer (Pinder & Grosse, 1991; Piovezan et al., 2010), our high density estimate within a forestry plantation is unexpected. At least two factors could have contributed to this finding: the modified landscape, and low hunting or predation pressure.

The development of commercial tree plantations and cattle pastures has been facilitated by water control structures, including embankments of 2–6 m above typical water levels, transforming embanked enclosures into flood-free land (Galafassi, 2005; Blanco & Méndez, 2010). As embankment enclosures are interspersed throughout the lower delta landscape (Minotti, 2019), they have increased the transitional areas between open water and terrestrial uplands preferred by the marsh deer (Piovezan et al., 2010). El Oasis is completely embanked and because of its relatively large size (> 100 km²) it contains a heterogeneous landscape. Although forest plantations dominate, these comprise various tree species (but mostly willow, which has been shown to provide better habitat for wildlife than poplar, eucalyptus or pines in this wetland; Varela, 2003; Fracassi & Somma, 2010) of heterogeneous ages and differing management stages. Plantations, numerous streams, artificial channels and small marshlands are embedded within this landscape, and this has resulted in areas of high plant diversity, including a community of macrophytes (i.e. aquatic plants that grow in or near water), the main food of marsh deer in this delta (Marin et al., 2020). Consequently, this modified landscape appears to offer marsh deer both suitable forage and habitat conditions.

As with most large herbivores (Ripple et al., 2015), poaching is one of the main threats to marsh deer in the lower delta (Pereira et al., 2019). The impact of this, however, varies widely throughout the region; anti-poaching controls by governmental authorities are generally insufficient or non-existent and consequently anti-poaching measures are dependent on individual properties. Large forestry properties within the delta usually employ simple poaching controls such as occasional patrols or gates with padlocks, to prevent vehicular access (JAP, pers. obs., 2020). Protection in El Oasis is through daily patrols by contracted guards, who also control access to the property at entrances. However, isolated cases of marsh deer poaching still occur (D. Artero, pers. comm., 2020). The high population density of marsh deer that we recorded could be a result of low hunting pressure, the absence of natural predators and domestic dogs, and the high primary productivity. This is plausible as small, well-protected, food-rich areas have been observed to be important for facilitating recovery of populations of other ungulate species following the cessation of poaching (Steinmetz et al., 2010).

The contribution of private lands to biodiversity conservation has been underappreciated (Davies-Mostert, 2014), although they play a key role in ungulate conservation (East, 1999; Hoffmann et al., 2015). The high density of marsh deer recorded in the plantation matrix of the study area, together with reduced mortality and an apparently high fawn recruitment (authors, pers. obs., 2020) suggest that the marsh deer subpopulation inhabiting this large property could be contributing to maintenance of the population in the wider landscape. Immigration of individuals from source populations is important for replenishing populations of ungulates affected by overhunting and/or low habitat quality (Novaro et al., 2000; Seydack et al., 2000; Naranjo & Bodmer, 2007; Vongkhamheng et al., 2013). As the lower delta is being modified rapidly (mostly to develop pastures for cattle ranching; Sica et al., 2016) and poaching is widespread in this wetland (Pereira et al., 2019), the potential role of El Oasis as a source of marsh deer should be evaluated and considered as part of the conservation strategy for this population.

We were able to capture high-resolution imagery of marsh deer with UAVs, and to detect individual deer from photographs taken at an altitude of 45 m. Marsh deer did not appear to respond to UAVs, a matter also noted for other ungulates (Christie et al., 2016). This is a potential advantage of surveys with UAVs, although further examination of this is needed under a range of circumstances (Schroeder et al., 2020). We designed the survey to minimize sampling errors and biases in estimating abundance, such as not detecting an individual that was actually present or double counting individuals (Brack et al., 2018). Firstly, flights were conducted during winter, when individuals were most exposed as canopy cover is at its lowest. Nevertheless, some deer could have been present in the surveyed area but unavailable for detection (e.g. hidden beneath bushes), contributing to availability bias (Brack et al., 2018). As demonstrated for other mammal species, adjusting for availability bias can produce substantially larger and less biased abundance estimates (Pollock et al., 2006; Heide-Jørgensen & Laidre, 2015; Sucunza et al., 2018). Consequently, addressing availability bias in any future surveys of marsh deer with drones, by incorporating auxiliary information (e.g. telemetry data, ground-based surveys) or using temporally replicated flights (Brack et al., 2018), could produce more accurate and precise density estimates. Secondly, a multiple-observer protocol was employed to minimize failures to detect individuals during the manual analysis of the photographs. Thirdly, double counts of individuals in overlapped sequential images were avoided by analysing successive images. However, the manual examination of photographs was time consuming. The use of computer recognition algorithms (Torney et al., 2016; Corcoran et al., 2021) to automate the detection of marsh deer from photographs could potentially decrease the time required for image analysis.

Marsh deer in the lower delta of the Paraná River are exploiting a matrix of commercial tree plantations, and new dietary resources (invasive exotic plant species; Marin et al., 2020), matters that have not been observed elsewhere in the species' range. This apparent ecological flexibility of the marsh deer may provide it with greater resilience to land-use pressures in the study region. By 2050, habitat for mammals is expected to decline by 5–16% globally compared to 2015 levels, with South America one of the regions most affected (Baisero et al., 2020). To promote sustainable forestry production in the lower delta and facilitate the conservation of the marsh deer, measures focused on building consensus among key regional stakeholders (Fracassi et al., 2017), the use of forestry practices adapted to local conditions (Fracassi et al., 2014), the promotion of interdisciplinary research to generate robust data (Pereira et al., 2018), and the employment of mechanisms to increase the value of the species (such as the FSC ecosystems services certificate obtained by El Oasis for the conservation of the marsh deer) are needed. Such actions, along with appropriate design and management of commercial tree plantations and other private lands, offer an opportunity for the conservation of this population of the Vulnerable marsh deer. Protection of the remaining native marshlands and restoration of the original woodlands will also be necessary to maintain the integrity of co-evolved plant–herbivore interactions in this wetland.

Acknowledgements We thank the volunteers who took part in this research (G. Aguirre, D. Alercia, L. Araki, L. Bazán, J. Becerra Ruiz, A. Bellotti, M. Cabrera, J. Capiello, A. Cardón, P. Casco, F. Castro, L. Cocchiararo, C. Condomiña, M. D'Occhio, C. Esponda, M. Falcón, A. Fanloo, A. Forlenza, F. Frattini, J. Galiano, M. Garbalena, N. García del Castello, J. Ghiorzo, V. Lafarga, B. Malagisi, M. Mieres, A. Olivera, G. Pace, O. Pacheco, S. Palomeque, B. Pérez, N. Rodríguez, P. Rodríguez, I. Rueda, S. Saavedra, R. Sánchez, L. Smith, M. Vázquez and F. Viviani); Arauco Argentina S.A., and particularly Diego Artero, for research permits and logistical support; Fundación Ambiente y Recursos Naturales and Toyota Argentina S.A. for financial support; and Jeffrey J. Thompson and two anonymous reviewers for constructive comments.

Author contributions Conception of the project idea, data analysis: JP, DV, CP; study design, fieldwork, writing: all authors.

Conflicts of interest None.

Ethical standards This study abided by the *Oryx* guidelines on ethical standards and did not involve human subjects or collection of specimens.

References

- ANDRIOLO, A., PIOVEZAN, U., COSTA, M.J.R.P., LAAKE, J. & DUARTE, J.M.B. (2005) Aerial line transect survey to estimate abundance of marsh deer (*Blastocercus dichotomus*) (Illiger, 1815). *Brazilian Archives of Biology and Technology*, 48, 807–814.

- ANDRIOLO, A., PIOVEZAN, U., COSTA, M.J.R.P., TORRES, H.A., VOGLIOTTI, A., ZERBINI, A.N. & DUARTE, J.M.B. (2013) Severe population decline of marsh deer, *Blastocerus dichotomus* (Cetartiodactyla: Cervidae), a threatened species, caused by flooding related to a hydroelectric power plant. *Zoologia*, 30, 630–638.
- ÁVILA, A.B. (2017) *Evaluación de un método de monitoreo aéreo de fauna mediante fotografía en los Esteros del Iberá (Corrientes, Argentina)*. MSc thesis. Universidad Nacional de Córdoba, Córdoba, Argentina.
- AYALA-CRESPO, J.M. (2010) Relevamiento poblacional del ciervo de los pantanos (*Blastocerus dichotomus*) en las pampas del Heath, Parque Madidi, Provincia Iturrealde, La Paz, Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental*, 28, 59–71.
- BAIGÚN, C.R.M., PUIG, A., MINOTTI, P.G., KANDUS, P., QUINTANA, R.D., VICARI, R. et al. (2008) Resource use in the Parana River Delta (Argentina): moving away from an ecohydrological approach? *Ecohydrology & Hydrobiology*, 8, 245–262.
- BAISERO, D., VISCONTI, P., PACIFICI, M., CIMATTI, M. & RONDININI, C. (2020) Projected global loss of mammal habitat due to land-use and climate change. *One Earth*, 2, 578–585.
- BARTMANN, R.M., CARPENTER, L.H., GARROTT, R.A. & BOWDEN, D.C. (1986) Accuracy of helicopter counts of mule deer in pinyon-juniper woodland. *Wildlife Society Bulletin*, 14, 356–363.
- BEASOM, S.L., LEON III, F.G. & SYNATZSKE, D.R. (1986) Accuracy and precision of counting white-tailed deer with helicopters at different sampling intensities. *Wildlife Society Bulletin*, 14, 364–368.
- BECCACECI, M.D. (1994) A census of marsh deer in Iberá Natural Reserve, its Argentine stronghold. *Oryx*, 28, 131–134.
- BECCACECI, M.D. (1996) Dieta del ciervo de los pantanos, *Blastocerus dichotomus*, en la reserva del Iberá, Corrientes, Argentina. *Mastozoología Neotropical*, 3, 193–197.
- BLANCO, D.E. & MÉNDEZ, F.M. (eds) (2010) *Endicamientos y Terraplenes en el Delta del Paraná: Situación, Efectos Ambientales y Marco Jurídico*. Fundación para la Conservación y el Uso Sustentable de los Humedales, Buenos Aires, Argentina.
- BRACK, I.V., KINDEL, A. & OLIVEIRA, L.F.B. (2018) Detection errors in wildlife abundance estimates from Unmanned Aerial Systems (UAS) surveys: Synthesis, solutions, and challenges. *Methods in Ecology and Evolution*, 9, 1864–1873.
- CAUGHLEY, G. (1974) Bias in aerial survey. *The Journal of Wildlife Management*, 38, 921–933.
- CAUGHLEY, G. & GRIGG, G.C. (1981) Surveys of the distribution and density of kangaroos in the pastoral zone of South Australia, and their bearing on the feasibility of aerial survey in large and remote areas. *Australian Wildlife Research*, 8, 1–12.
- CHABOT, D. & BIRD, D.M. (2015) Wildlife research and management methods in the 21st century: where do unmanned aircraft fit in? *Journal of Unmanned Vehicle Systems*, 3, 137–155.
- CHRISTIE, K.S., GILBERT, S.L., BROWN, C.L., HATFIELD, M. & HANSON, L. (2016) Unmanned aircraft systems in wildlife research: current and future applications of a transformative technology. *Frontiers in Ecology and the Environment*, 14, 241–251.
- CORCORAN, E., WINSEN, M., SUDHOLZ, A. & HAMILTON, G. (2021) Automated detection of wildlife using drones: synthesis, opportunities and constraints. *Methods in Ecology and Evolution*, 12, 1103–1114.
- COSTA, S.S., OLIVEIRA, D.B., MANCO, A.M., DEMELO, G.O., CORDEIRO, J.L.P., ZANIOLO, S. et al. (2006) Plants composing the diet of marsh and pampas deer in the Brazilian Pantanal wetland and their ethnomedicinal properties. *Journal of Biological Sciences*, 6, 840–846.
- D'ALESSIO, S., LARTIGAU, B., APRILE, G., HERRERA, P., VARELA, D., GAGLIARDI, F. & MÓNACO, C. (2006) Distribución, abundancia relativa y acciones para la conservación del ciervo de los pantanos en el Bajo Delta del río Paraná. In *Humedales Fluviales de América del Sur. Hacia un Manejo Sustentable* (eds J. Petean & J. Cappato), pp. 129–153. Proteger Ediciones, Santa Fe, Argentina.
- DAVIES-MOSTERT, H.T. (2014) Overcoming barriers to understanding the biodiversity contribution of private ranchlands. *Animal Conservation*, 17, 399–400.
- DE MELO, F.R. (2021) Drones for conservation: new techniques to monitor muriquis. *Oryx*, 55, 171.
- DUARTE, J.M.B., VARELA, D., PIOVEZAN, U., BECCACECI, M.D. & GARCÍA, J.E. (2016) *Blastocerus dichotomus*. In *The IUCN Red List of Threatened Species* 2016. [dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T2828A22160916.en](https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T2828A22160916.en).
- EAST, R. (1999) African Antelope Database 1998. *Occasional Paper of the IUCN Species Survival Commission*, 21.
- FLEMING, P.J.S. & TRACEY, J.P. (2008) Some human, aircraft and animal factors affecting aerial surveys: how to enumerate animals from the air. *Wildlife Research*, 35, 258–267.
- FRACASSI, N.G., PEREIRA, J.A., MUJICA, G., HAURI, B. & QUINTANA, R.D. (2017) Estrategias de conservación de la biodiversidad en paisajes forestales del Bajo Delta del Paraná—Uniendo a los actores clave de la región. *Mastozoología Neotropical*, 24, 59–68.
- FRACASSI, N.G., QUINTANA, R.D., PEREIRA, J.A. & MUJICA, G. (2014) *Estrategias de Conservación de la Biodiversidad en Plantaciones Forestales de Salicáceas del Bajo Delta del Paraná*. Ediciones INTA, Buenos Aires, Argentina.
- FRACASSI, N.G. & SOMMA, D.J. (2010) Participatory action research concerning the landscape use by a native cervid in a wetland of the Plata Basin, Argentina. *IUFRO-IALE International Conference 'Landscapes Forest and Global Change: New Frontiers in Management, Conservation and Restoration'*. Book of Abstracts, pp. 168–169. Bragança, Portugal.
- GALAFASSI, G. (2005) *La Pampeanización del Delta. Sociología e Historia del Proceso de Transformación Productiva, Social y Ambiental del Bajo Delta del Paraná*. Ediciones Extramuros, Buenos Aires, Argentina.
- GUO, X., SHAO, Q., LI, Y., WANG, D., LIU, J. et al. (2018) Application of UAV remote sensing for a population census of large wild herbivores—Taking the headwater region of the Yellow River as an example. *Remote Sensing*, 10, 1041.
- HAHN, N., MWAKATOBÉ, A., KONUCHE, J., DE SOUZA, N., KEYU, J., GOSS, M. et al. (2017) Unmanned aerial vehicles mitigate human–elephant conflict on the borders of Tanzanian Parks: a case study. *Oryx*, 51, 513–516.
- HEIDE-JØRGENSEN, M.P. & LAIDRE, K.L. (2015) Surfacing time, availability bias and abundance of humpback whales in West Greenland. *Journal of Cetacean Research and Management*, 15, 1–8.
- HODGSON, J.C. & KOH, L.P. (2016) Best practice for minimising unmanned aerial vehicle disturbance to wildlife in biological field research. *Current Biology*, 26, 404–405.
- HODGSON, J.C., MOTT, R., BAYLIS, S.M., PHAM, T.T., WOTHERSPOON, S., KILPATRICK, A.D. et al. (2018) Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution*, 9, 1160–1167.
- HOFFMANN, M., DUCKWORTH, J.W., HOLMES, K., MALLON, D.P., RODRIGUES, A.S.L. & STUART, S.N. (2015) The difference conservation makes to extinction risk of the world's ungulates. *Conservation Biology*, 29, 1303–1313.
- HU, J., WU, X. & DAI, M. (2020) Estimating the population size of migrating Tibetan antelopes *Pantholops hodgsonii* with unmanned aerial vehicles. *Oryx*, 54, 101–109.
- IEZZI, M.E., FRACASSI, N.G. & PEREIRA, J.A. (2018) Conservation of the largest cervid of South America: interactions between people and the Vulnerable marsh deer *Blastocerus dichotomus*. *Oryx*, 52, 654–660.

- JACHMANN, H. (2001) *Estimating Abundance of African Wildlife: An Aid to Adaptive Management*. Kluwer Academic Publishers, Boston, USA.
- LARTIGAU, B., DE ANGELO, C., D'ALESSIO, S., JIMÉNEZ PÉREZ, I., APRILE, G., AUED, M.B. & FRACASSI, N.G. (2012) *Blastocerus dichotomus*. In *Libro Rojo de los Mamíferos Amenazados de la Argentina* (eds R. Ojeda, V. Chillo & G.B. Díaz Isenrath), pp. 121–124. Sociedad Argentina para el Estudio de los Mamíferos, Mendoza, Argentina.
- LINCHANT, J., LHOEST, S., QUEVAUVILLERS, S., LEJEUNE, P., VERMEULEN, C., SEMEKI NGABINZEKE, J. et al. (2018) UAS imagery reveals new survey opportunities for counting hippos. *PLOS ONE*, 13, e0206413.
- MARIN, V.C., FERNÁNDEZ, V.A., DACAR, M.A., GUTIÉRREZ, D.G., FERGNANI, D. & PEREIRA, J.A. (2020) Diet of the marsh deer in the Delta of the Paraná River, Argentina—a vulnerable species in a productive context. *European Journal of Wildlife Research*, 66, 16.
- MÁRQUEZ, A., MALDONADO, J.E., GONZÁLEZ, S., BECCACECI, M.D., GARCÍA, J.E. & DUARTE, J.M.B. (2006) Phylogeography and Pleistocene demographic history of the endangered marsh deer (*Blastocerus dichotomus*) from the Río de la Plata Basin. *Conservation Genetics*, 7, 563–575.
- MAURO, R.A., MOURÃO, G.M., PEREIRA DA SILVA, M., COUTINHO, M.E., TOMAS, W.M. & MAGNUSSON, W.E. (1995) Influência do habitat na densidade e distribuição de cervo (*Blastocerus dichotomus*) durante a estação de seca no pantanal mato-grossense. *Revista Brasileira de Biologia*, 55, 745–751.
- MINOTTI, P. (2019) *Actualización y Profundización del Mapa de Endicamientos y Terraplenes de la Región del Delta del Paraná, 2018*. Wetlands International, Buenos Aires, Argentina.
- MOURÃO, G. & CAMPOS, Z. (1995) Survey of broad-snouted caiman *Caiman latirostris*, marsh deer *Blastocerus dichotomus* and capybara *Hydrochaeris hydrochaeris* in the area to be inundated by Porto Primavera Dam, Brazil. *Biological Conservation*, 73, 27–31.
- 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. *Biological Conservation*, 92, 175–183.
- NARANJO, E.J. & BODMER, R.E. (2007) Source–sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation*, 138, 412–420.
- NOVARO, A.J., REDFORD, K.H. & BODMER, R.E. (2000) Effect of hunting in source–sink systems in the Neotropics. *Conservation Biology*, 14, 713–721.
- OLIVEIRA-DA-COSTA, M., MARMONTEL, M., DA-ROSA, D.S.X., COELHO, A., WICH, S., MOSQUERA-GUERRA, F. & TRUJILLO, F. (2020) Effectiveness of unmanned aerial vehicles to detect Amazon dolphins. *Oryx*, 54, 696–698.
- PEREIRA, G.F. (2016) *Aplicação do sensoriamento remoto no levantamento da população de cervos do pantanal Blastocerus dichotomus (Illiger, 1815) na Fazenda Cisalpina, Mato Grosso do Sul*. MSc thesis. Instituto de Pesquisas Ecológicas, São Paulo, Brazil.
- PEREIRA, J.A., FERGNANI, D., FERNÁNDEZ, V., FRACASSI, N.G., GONZÁLEZ, V., LARTIGAU, B. et al. (2018) Introducing the “Pantano Project” to conserve the southernmost population of the marsh deer. *Deer Specialist Group Newsletter*, 30, 15–21.
- PEREIRA, J.A., VARELA, D., APRILE, G., CIRIGNOLI, S., OROZCO, M., LARTIGAU, B. et al. (2019) *Blastocerus dichotomus*. In *Categorización 2019 de los Mamíferos de Argentina Según su Riesgo de Extinción. Lista Roja de los Mamíferos de Argentina*. doi.org/10.31687/SaremLR.19.207 [accessed 7 December 2020].
- PERES, P.H.F., POLVERINI, M.S., OLIVEIRA, M.L. & DUARTE, J.M.B. (2017) Accessing camera trap survey feasibility for estimating *Blastocerus dichotomus* (Cetartiodactyla, Cervidae) demographic parameters. *Iheringia, Série Zoológica*, 107, e2017041.
- PINDER, L. (1996) Marsh deer *Blastocerus dichotomus* population estimate in the Paraná River, Brazil. *Biological Conservation*, 75, 87–91.
- PINDER, L. & GROSSE, A.P. (1991) *Blastocerus dichotomus*. *Mammalian Species*, 380, 1–4.
- PIOVEZAN, U. (2004) *História natural, área de vida, abundância de Blastocerus dichotomus (Illiger, 1815) (Mammalia Cervidae) e monitoramento de uma população à montante da Hidrelétrica Sergio Motta, Rio Paraná, Brasil*. PhD thesis. University of Brasília, Brasília, Brazil.
- PIOVEZAN, U., TIEPOLO, L.M., TOMAS, W.M., DUARTE, J.M.B., VARELA, D. & MARINHO-FILHO, J.S. (2010) Marsh deer *Blastocerus dichotomus* (Illiger, 1815). In *Neotropical Cervidology: Biology and Medicine of Latin American Deer* (eds J.M.B. Duarte & S. González), pp. 66–76. Funep/IUCN, Jaboticabal, Brazil.
- POLLOCK, K.H., MARSH, H.D., LAWLER, I.R. & ALLDREDGE, M.W. (2006) Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. *Journal of Wildlife Management*, 70, 255–262.
- PRESTON, T.M., WILDHABER, M.L., GREEN, N.S., ALBERS, J.L. & DEBENEDETTO, G.P. (2021) Enumerating white-tailed deer using unmanned aerial vehicles. *Wildlife Society Bulletin*, 45, 97–108.
- QGIS DEVELOPMENT TEAM (2020) QGIS. Open Source Geospatial Foundation Project. qgis.osgeo.org [accessed 18 November 2020].
- QUINTANA, R.D., BÓ, R.F., ASTRADA, E. & REEVES, C. (2014) *Lineamientos para una Ganadería Ambientalmente Sustentable en el Delta del Paraná*. Fundación Humedales/Wetlands International, Buenos Aires, Argentina.
- RIOS-UZEDA, B. & MOURÃO, G. (2012) Densities of the Vulnerable marsh deer *Blastocerus dichotomus* in Bolivia's northern savannahs. *Oryx*, 46, 260–265.
- RIPPLE, W.J., NEWSOME, T.M., WOLF, C., DIRZO, R., EVERATT, K.T., GALETTI, M. et al. (2015) Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.
- SAMUEL, M.D., GARTON, E.O., SCHLEGEL, M.W. & CARSON, R.G. (1987) Visibility bias during aerial surveys of elk in Northcentral Idaho. *Journal of Wildlife Management*, 51, 622–630.
- SANDBROOK, C. (2015) The social implications of using drones for biodiversity conservation. *Ambio*, 44, 636–647.
- SCARPA, L.J. & PIÑA, C.I. (2019) The use of drones for conservation: A methodological tool to survey caimans nests density. *Biological Conservation*, 238, 108235.
- SCHROEDER, N.M., PANEBIANCO, A., GONZÁLEZ MUSSO, R. & CARMANCAHI, P. (2020) An experimental approach to evaluate the potential of drones in terrestrial mammal research: a gregarious ungulate as a study model. *Royal Society Open Science*, 7, 191482.
- SEYDACK, A.H.W., VERMEULEN, C. & HUISAMEN, J. (2000) Habitat quality and the decline of an African elephant population: implications for conservation. *South African Journal of Wildlife Research*, 30, 34–42.
- SICA, Y.V., QUINTANA, R.D., RADELOFF, V.C. & GAVIER-PIZARRO, G.I. (2016) Wetland loss due to land use change in the lower Paraná River Delta, Argentina. *Science of the Total Environment*, 568, 967–978.
- SINCLAIR, A.R.E. (1972) Long term monitoring of mammal populations in the Serengeti: census of non-migratory ungulates, 1971. *African Journal of Ecology*, 10, 287–297.
- STEINMETZ, R., CHUTIPONG, W., SEUATURURIEN, N., CHIRNGSAARD, E. & KHAENGKHEKARN, M. (2010) Population recovery patterns of Southeast Asian ungulates after poaching. *Biological Conservation*, 143, 42–51.

- SUCUNZA, F., DANILEWICZ, D., CREMER, M., ANDRIOLO, A. & ZERBINI, A.N. (2018) Refining estimates of availability bias to improve assessments of the conservation status of an endangered dolphin. *PLOS ONE*, 13, e0194213.
- TIEPOLO, L.M., TOMAS, W.M. & LIMA-BORGES, P.A. (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, 111–115.
- TOMAS, W.M. & SALIS, S.M. (2000) Diet of the marsh deer (*Blastocerus dichotomus*) in the Pantanal wetland, Brazil. *Studies on Neotropical Fauna and Environment*, 35, 165–172.
- TOMAS, W.M., SALIS, S.M., SILVA, M.P. & MOURÃO, G.M. (2001) Marsh deer (*Blastocerus dichotomus*) distribution as a function of floods in the Pantanal wetland, Brazil. *Studies on Neotropical Fauna and Environment*, 36, 9–13.
- TORNEY, C.J., DOBSON, A.P., BORNER, F., LLOYDJONES, D.J., MOYER, D., MALITI, H.T. et al. (2016) Assessing rotation-invariant feature classification for automated wildebeest population counts. *PLOS ONE*, 11, e0156342.
- VARELA, D. (2003) *Distribución, Abundancia y Conservación del Ciervo de los Pantanos (Blastocerus dichotomus) en el Bajo Delta del Río Paraná, Provincia de Buenos Aires, Argentina*. BSc thesis. Universidad de Buenos Aires, Buenos Aires, Argentina.
- VERMEULEN, C., LEJEUNE, P., LISEIN, J., SAWADOGO, P. & BOUCHE, P. (2013) Unmanned aerial survey of elephants. *PLOS ONE*, 8, e54700.
- VONGKHAMHENG, C., JOHNSON, A. & SUNQUIST, M. (2013) A baseline survey of ungulate abundance and distribution in northern Lao: implications for conservation. *Oryx*, 47, 544–552.
- WANG, D., SHAO, Q. & YUE, H. (2019) Surveying wild animals from satellites, manned aircraft and unmanned aerial systems (UASs): a review. *Remote Sensing*, 11, 1308.