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Article

EXTREME FLOODING INCREASES POACHING MORTALITY IN THE SOUTHERNMOST STRONGHOLD OF THE ENDANGERED MARSH DEER

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ABSTRACT. Extreme stochastic perturbations can affect population dynamics, but quantitative assessments are scarce for threatened species. The 2015-2016 El Niño-Southern Oscillation (ENSO) caused extreme flooding in the Delta of the Paraná River in Argentina where the southernmost population of the regionally endangered marsh deer (*Blastocerus dichotomus*) occurs. Using field surveys and data from informants, we studied the impact of this flood on the mortality, distribution, and abundance of this marsh deer population in an area of 1 236 km^2. The occurrence of this extreme flood significantly increased marsh deer mortality. One hundred forty-two marsh deer deaths were recorded over the seven-month flood duration, with poaching accounting for 86.6% of deaths. Mortality of marsh deer was significantly higher near urban areas, embankments, and dirt roads, while mortality from poaching was higher in plantations and permanently inundated lands. Two areas of high spatial clustering of poaching mortality were detected, encompassing plantations with easy access or in proximity to urban areas, while embankments appeared to act as attractive population sinks. Flood-related mortality significantly decreased the occurrence of the species in the study area after the flood, but changes in relative abundance between periods were heterogeneous across the landscape, probably because of local migrations. Since climate change is expected to increase the global frequency and magnitude of extreme flood events, our study provides valuable information for mitigating the negative synergistic effects of extreme flooding on marsh deer, as well as for global wildlife populations subjected to periodic extreme floods.

RESUMEN. LAS INUNDACIONES EXTREMAS INCREMENTAN LA MORTALIDAD POR CACERÍA EN EL REFUGIO MÁS AUSTRAL DEL AMENAZADO CIERVO DE LOS PANTANOS. Las perturbaciones estocásticas extremas pueden afectar la dinámica de las poblaciones, pero las evaluaciones cuantitativas son escasas para las especies amenazadas. El fenómeno de "El Niño" de 2015-2016 causó inundaciones extremas en el Delta del río Paraná en Argentina, donde se encuentra la población más austral del ciervo de los pantanos (*Blastocerus dichotomus*), categorizada como En Peligro a nivel regional. En base a relevamientos de campo y

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datos de informantes, estudiamos el impacto de esta inundación sobre la mortalidad, distribución y abundancia de esta población de ciervo de los pantanos dentro de un área de 1 236 km^2. La ocurrencia de esta inundación incrementó significativamente la mortalidad del ciervo de los pantanos. Hemos registrado 142 individuos muertos durante los siete meses de duración de la inundación, y la caza furtiva representó el 86.6% de las muertes. La mortalidad del ciervo de los pantanos fue significativamente mayor en proximidad a áreas urbanas, terraplenes y caminos vehiculares, mientras que la mortalidad por cacería fue mayor en plantaciones y terrenos permanentemente inundados. Se detectaron dos áreas de alta concentración espacial de mortalidad por cacería, que abarcaron plantaciones de fácil acceso o próximas a áreas urbanas, mientras que los terraplenes parecen haber funcionado como sumideros atractivos para los ciervos. La mortalidad relacionada con las inundaciones disminuyó significativamente la presencia de la especie dentro del área de estudio luego de la inundación, pero los cambios en la abundancia relativa entre períodos fueron heterogéneos en todo el paisaje, probablemente como resultado de migraciones locales. Dado que se espera que el cambio climático aumente la frecuencia global y la magnitud de las inundaciones extremas, nuestro estudio proporciona información valiosa para mitigar los efectos sinérgicos negativos de las inundaciones extremas tanto en el ciervo de los pantanos como en poblaciones de otras especies sujetas a inundaciones extremas periódicas.

Key words: *Blastocerus dichotomus*, Delta of Paraná River, El Niño-Southern Oscillation, Refuge migration, wetlands.

Palabras clave: *Blastocerus dichotomus*, Delta del río Paraná, El Niño-Oscilación del Sur, humedales, migración por refugio.

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INTRODUCTION

Extreme stochastic perturbations such as massive floods, volcanic eruptions, heat waves, or severe droughts have the potential to affect population dynamics and drive community structure (Parmesan et al. 2000; Holmgren et al. 2006; Sergio et al. 2018). Extreme perturbations can affect vast areas and cause major changes in landscapes and vegetation, alter animal behavioral patterns and reduce animal population sizes, even causing local extinctions (e.g., Waite et al. 2007; Maxwell et al. 2018; Abernathy et al. 2019; Pruvot et al. 2019). The impact of an extreme perturbation can increase when it co-occurs with other processes, acting additively or synergistically, resulting in greater effects on populations or communities than when these events occur in isolation (Geary et al. 2019). However, since extreme perturbations are rare or unpredictable, studies to record their interaction with other processes are infrequent and usually complicated in terms of sampling design (i.e., sample sizes and replications). As a result, the effects of the interaction of rare catastrophic events with other processes on populations or community dynamics are poorly documented (often accidentally, during research focused on other topics) and misunderstood.

Extreme floods are recognized as a source of massive mortality in mammalian populations (Heinen & Singh 2001; Thibault & Brown 2008; Wuczynski & Jakubiec 2013; Ugarković et al. 2019), and the magnitude of their effect depends on several issues, including the life history strategy of the species, age and sex of individuals, the extent of the flooded area, and the duration of flooding (Heinen 1993; Jacob 2003; Thibault & Brown 2008; Wuczynski & Jakubiec 2013). Drowning is usually an important cause of mortality of mammals during these events (Thibault & Brown 2008; Wuczynski & Jakubiec 2013), but other factors such as diseases or hunting/poaching can also interact to increase mortality rates (e.g., Schaller & Vasconcelos 1978; Bodmer et al. 2017; Orozco et al. 2020). Despite the implications that the co-occurrence of extreme floods and other threats can have for the conservation of mammal species or populations, quantitative assessments have been mostly focused on common or abundant species. Rare or threatened species may show different responses to these events, experiencing habitat loss by inundation and associated mortality in different ways (e.g., as a catastrophe). On the other hand, the impacts of such perturbations are particularly informative when they involve large-bodied mammals

(> 3 kg body mass), because this group of species is at higher risk of extinction due to both environmental factors and intrinsic biological traits (Cardillo et al. 2005; Ripple et al. 2016).

Marsh deer (*Blastocerus dichotomus*), the largest (80-150 kg body mass) native cervid of South America, is considered Vulnerable (Duarte et al. 2016) after experiencing a reduction of 65% of its range (Weber & González 2003). It is distributed from central Brazil to central Argentina and is one of the few deer species restricted to wetlands and riverine areas (Piovezan et al. 2010). To cope with the seasonally flooded habitat that characterizes most of its range, marsh deer make local migratory movements according to the hydrological cycle of seasonal floods (Schaller & Vasconcelos 1978; Tomas et al. 2001). In addition, the species is capable of using large areas with thick floating marsh as a refuge during floods (Piovezan et al. 2010; D'alessio 2016). Despite their morphological and behavioral adaptations to wetlands, extreme flooding events in combination with other factors can still negatively impact populations. For example, flooding caused by a dam closure in Brazil resulted in habitat loss that led to a 54% drop in marsh deer abundance due to the direct impact of flooding and associated factors such as increased disease and hunting and decreased food availability (Andriolo et al. 2013). Poaching in the middle basin of the Paraná River in Northern Argentina was also responsible for the high marsh deer mortality during the extreme flooding in 1982-1983 (Giraudo & Arzamendia 2008).

The southernmost population of the marsh deer occurs in the Delta of the Paraná River (Varela 2003), the lowest section of one of the largest rivers in South America. The habitat of this deer population is subjected to ordinary (i.e., daily, and seasonal) floods and, at greater intervals, to extreme inundations triggered by the El Niño-Southern Oscillation (ENSO; Bonetto et al. 1986; Prieto 2007). Massive poaching mortality of marsh deer during extreme floods has been historically recorded in local literature (Lynch-Arribálzaga 1878; Garra 1955) and has also been recently observed by locals (authors, unpublished data). Although it has been hypothesized that massive mortality during these extreme floods could dramatically affect marsh deer population dynamics (Varela 2003; D'alessio 2016), population declines after extreme floods have not been quantified. Considering the limited distribution of the marsh deer population in the Delta of the Paraná River (< 2 700 km^2), threats from various sources (e.g., poaching, retaliatory killings to protect tree plantations, habitat loss, and predation by dogs), and its genetic singularity in comparison with other populations (Márquez et al. 2006), the conservation status of the marsh deer population inhabiting this wetland has been categorized as Endangered (Pereira et al. 2019).

The 2015-2016 ENSO was the first extreme climatic event of the 21st century and one of the strongest since records began, rivaling those occurring in 1982-1983 and 1997-1998 (McPhaden et al. 2020). This ENSO event caused extreme flooding in the lower Paraná River from late December 2015 to early June 2016, inundating large areas with depths of up to 2 m (INTA 2016). We studied the impact of flood-related threats (natural and anthropogenic) from this event on marsh deer mortality, distribution, and abundance patterns by (1) estimating the minimum number of marsh deer that died in this population during the 2015-2016 extreme flood; (2) assessing the impact of poaching during the flood; (3) analyzing the spatial patterns of marsh deer mortality within the study area; and (4) assessing the distribution and abundance of marsh deer within the study area before and after the 2015-2016 extreme flood. In addition, we documented marsh deer mortality outside of extreme flood periods for comparison. Since climate forecasts predict a doubling of the occurrence of extreme ENSO events in response to global climate change (Cai et al. 2014) and an increase in global exposure to flooding (Milly et al. 2002; Hirabayashi et al. 2013), it is expected that more frequent and lasting fluvial flooding events will occur in the lower Paraná River basin (Camilloni et al. 2013). Given this expected scenario, understanding the effects of co-occurring natural and human-related threats is of utmost importance for the conservation of the marsh deer in the lower Delta of the Paraná River and throughout the range of the species, as well as for other species living in areas subject to similar disturbances.

MATERIALS AND METHODS

Study area

The lower Delta of the Paraná River (hereafter, "lower Delta") is located in the lower reach of the Paraná River and the upper part of the Rio de la Plata estuary in Argentina (**Fig.** 1a). This wetland exhibits marked environmental heterogeneity (Kandus & Malvárez 2004) and is subject to a hydrological regime affected by large rivers (e.g., Paraná, Uruguay), tidal and storm surges from the Rio de la Plata estuary, as well as local rainfall (Baigún et al. 2008). Moderate floods occur several times per year in this delta, but extreme floods (i.e., flood discharge of > 33 000 $m^3 s^{-1}$) have an average recurrence period of up to 15 years. The original physiognomy of this wetland (characterized mainly by freshwater marshes and riparian forests; Kandus & Malvárez 2004) has experienced large-scale transformation, primarily by the draining of freshwater marshes and flood control embankments to safeguard commercial tree plantations and facilitate livestock production (Galafassi 2004; Sica et al. 2016). The height of embankments can range from 2 to 6 meters above the mean water level.

Between late December 2015 and early June 2016, the lower Delta was affected by flooding initiated by rainfall throughout the Paraná River watershed, with an exceptional period of heavy rainfall occurring between 15 and 18 April in the study area (representing 200% of the average rainfall for that month), followed by a wind tide (or "sudestada"; Escobar et al. 2004) that significantly raised water levels. A sub-region of about 950 km^2 of the lower Delta delimited by the National Road 12 to the west, the De la Serna channel to the east, and the Paraná Guazú and Paraná de las Palmas Rivers to the north and south, respectively (**Fig.** 1a), was particularly affected by this extreme flooding, with water stagnation lasting up to 4 months in low-lying zones. In this area, there was 1 077 km of embankments built, surrounding an area of about 566 km^2 (Minotti 2019).

Marsh deer were common and widespread in this area (Fracassi & Somma 2010; Iezzi et al. 2018), and we, therefore, chose it as our study area to assess marsh deer mortality, abundance, and distribution during the extreme 2015-2016 flood. In addition, an adjacent area of "riverside lowlands" (sensu Bonfils 1962), located to the south of the Paraná de las Palmas River was included in our study area (**Fig.** 1a) because marsh deer make migratory movements (refuge migration, sensu Gnanadesikan et al. 2017) toward the Pampean grasslands of this area during extreme flooding episodes (Garra 1955; Pereira et al. 2003). This area supports large urban areas, intensive agricultural activities, and industry with a population of nearly 430 000 (National Census 2010, https://www.indec.gob.ar). Our study area covered 1 236 km^2, mainly plantation forests and grazing lands, except for Ciervo de los Pantanos National Park, which occupies 55.8 km^2 in a marginal habitat area of wetlands and pampas surrounded by urban areas (**Fig.** 1a).

Field surveys to record marsh deer mortality during the 2015-2016 extreme flood. The study area was intensively surveyed between late December 2015 and early July 2016 both by vehicle (driving main and secondary dirt roads distributed throughout the entire sampling area) and by water (navigating the river courses, channels, or the flooded areas). The selection of the transport method depended on the availability of roads and river levels, as several roads were inundated at different times. These surveys were fairly homogeneously distributed throughout the study period, ranging from one (July) to five (January) surveys per month. During these surveys (n = 19; mean distance traveled per survey = 90.8 km; range = 54-149 km; total distance traveled = 1 726 km), it was possible to find dead marsh deer opportunistically or based on information from residents. When possible, the interiors of tree plantations were also sampled by opportunistically walking transects. Between six and 22 transects (length range = 50-450 m, based on plantation characteristics and water levels) were walked per survey. Positions of dead marsh deer were recorded using a GPS unit, and carcasses were subjected to external revision to determine the cause of death and, when possible, sex and age.

Finding carcasses during field surveys was highly opportunistic. Poachers usually removed the body of the killed animals or hid the unused parts of the carcasses, so the detectability of poached carcasses in the field was expected to be reduced. Similarly, scavengers could have consumed the carcasses, also contributing to lower detectability. Therefore, a complementary source of information based on reports from key informants was implemented to increase the number of marsh deer deaths recorded.

Information provided by key informants. After > 15 years of working in the area, a friendly relationship has developed with the residents (islanders), which aided our detection of marsh deer mortalities at the initial stage of the extreme flooding. Because the community of islanders is relatively small (< 3 000 people in our study area according to the National Census 2010) and well-connected, news and information usually spread rapidly within the lower Delta through informal word-of-mouth communication. To take advantage of this practice, nine individuals in the lower Delta were invited to contribute to this assessment by providing data on marsh deer mortality. They were instructed on how to collect the required information (see below) and asked to disseminate information about our initiative to their networks and social groups. Additional information was obtained through direct communication with other islanders or through social media.

Information on marsh deer mortalities collected through this method included: (1) date and location (as precise as possible) of the mortality event or location where the carcass was discovered; (2) cause of death attributed to the reported event (options: "poaching," "drowning," "predation by dogs," "poor body condition," "other" or "undetermined"); and (3) sex ("male," "female," "unknown") and age ("fawn," "juvenile," "adult" or "unknown"). Because informants would provide sensitive data in some cases (e.g., poaching activities), our survey was built to assure the full anonymity of the informants, avoiding a potential retaliatory action against the individuals involved. Thus, anyone who had data responding to the events in question was invited to submit their records directly to local referents or scientists via phone, e-mail, or a private message on social media (@proyectopantanoarg in Facebook), with anonymity guaranteed.

From February 2016 to April 2017, data were received from 162 informants (mainly locals, forest plantation owners, and employees of forestry companies, but also workers of transport companies, members of law enforcement, and people from local public institutions). All data provided were evaluated for reliability (i.e., how true the data were) by communicating with each informant after receiving the information. Questions were tailored to informants to avoid confusion, which was aided by our familiarity with the geography of the study area and local culture to accurately interpret the responses. When available, pictures of the dead animal(s) were used to confirm mortalities. When the data provided were not convincing, additional information was requested or, whenever possible, a cross-check was made with data provided by other informants to verify the records. If doubts persisted, the data were discarded (n = 12 discarded reports). On the other hand, the independence of each record was assessed to avoid overestimating the

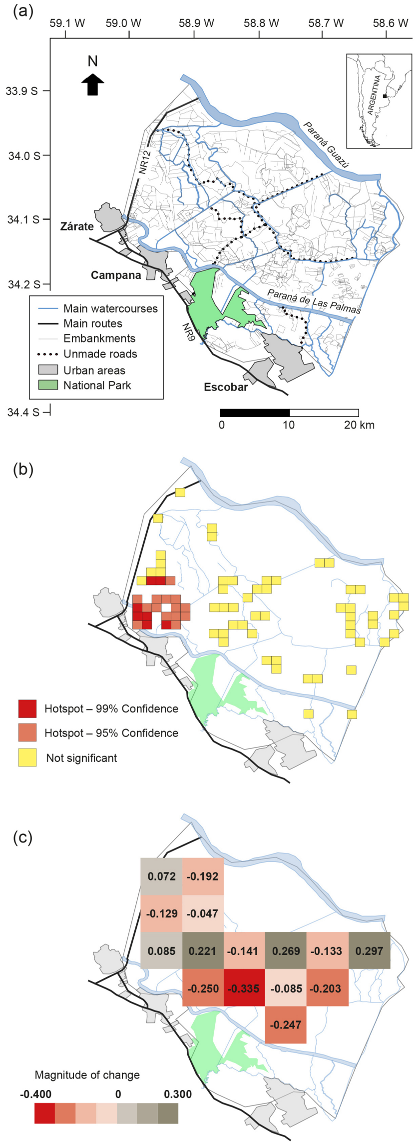

Fig. 1. (a) The study area in the lower Delta of the Paraná River and riverside lowlands, Argentina, including the main urban areas located in adjacent Pampas grasslands. (b) Marsh deer poaching hotspots identified during the 2015-2016 extreme flood. "Hotspots" represent areas with significant clustering (Getis Ord Statistic Z scores) of poaching events at different significance levels (99% and 95%); the hotspot model ignores those areas where poaching records were not documented. (c) Estimated changes in minimum relative abundance index (MRAI) of marsh deer between before and after the 2015-2016 extreme flood based on sign surveys conducted in 15 6 x 6-km grid cells during both periods.

number of marsh deer deaths (i.e., avoid more than one report of the same mortality) by comparing the location, date, and associated information of each mortality record (e.g., people involved, characteristics of animals). Assessing the reliability and independence of the data was a critical aspect of our work, as most of the mortality records we collected consisted of these data (see Results).

Spatial analysis of mortality data. A generalized additive model (GAM) with binomial response was fitted to the locations of recorded poaching mortalities in relationship to environmental covariates. We choose to use a GAM because it does not assume a fixed linear or other parametric forms of the relationship between the dependent variable and the covariates, does not assume *a* *priori* any specific form of that relationship, and can be used to reveal and estimate nonlinear effects of the covariate on the dependent variable (Wood 2017). The default Un-Biased Risk Estimator (UBRE) was used as the smoothness selection criteria. The alpha level to consider a smooth term as significant was set at 0.05. Although probability values for smooth terms in GAMs are approximate and may underestimate true probabilities (Zuur et al. 2009), for the sample size and binary response used in our analysis it has been shown that nominal coverage probabilities are attained (Wood 2013).

Covariates included in our modeling were land cover types (permanent water bodies, poplar and willow plantations, marshes with 10%-30% tree cover, marshes with 30%-60% tree cover, grasslands, and permanently inundated lands with 30%-60% water cover and > 10% vegetated cover; redefined from Hansen et al. 2000), elevation above sea level (in meters), slope (in radians), aspect (in radians), distance to urban areas (in meters), distance to rivers and other watercourses (in meters), distance to dirt roads (in meters), distance to embankments (in meters), and the percentage of the flooded area at the time of highest flooding during 2016 (see **Table** 3 for the observed ranges of these covariates). Land cover types were extracted from the summary MODIS C6MCD12Q1 product for the year 2016. Elevation was extracted from 5 SRTM 1-arc-second DEMs downloaded from Earth Explorer (https://earthexplorer.usgs.gov/) and slope and aspect were derived from the DEMs using the raster package in R (Hijmans 2020). The percentage of flooded areas at the 2016 flooding peak was extracted from spatial layers from the NRT Flood Mapping webpage (https://floodmap.modaps.eosdis.nasa.gov/). The locations of rivers, roads, urban areas, and embankments were digitized from Google Earth imagery from 2015 or provided by Minotti (2019), while distances from these features were generated with the "distance" function of the raster package (Hijmans 2020). A spatial resolution of 30 m was used because the original DEM had this resolution and the derived variables (aspect, slope) were generated with this resolution. Variables at other resolutions were projected to 30 m.

Covariate values from spatial data were extracted for the locations of registered marsh deer mortalities and a set of random points. Random points (n = double the number of recorded deaths) were selected with the "randomPoints" function in the R package "dismo" (Hijmans et al. 2021) excluding a 250 m radius of each recorded marsh deer mortality and urban areas. A response variable was assigned a value of 1 for coordinates where dead marsh deer were recorded and 0 for random points. The complexity of the GAM model was constrained by setting the number of knots for the smooth terms equal to 3, such that nonlinear relationships between predictors and the response variable were limited to simple trends (monotonic increase or decrease, increase, or decrease plus plateau, increase-decrease, and decrease-increase) (Wood 2017). The analysis was performed with R 4.0.3 (R-Project 2021) with the mgcv (Wood 2017) and visreg (Breheny & Burchett 2017) packages for model fitting and to visualize the partial effects of variables.

In addition, an optimized hotspot analysis using the Getis-Ord Gi* test (Getis & Ord 1992) was performed in ArcGIS 10.3.1 using the Optimized Hotspot Analysis tool based on the pooled mortality records to identify statistically significant mortality hotspots. The Optimized Hotspot Analysis tool aggregates incident data into fishnet (grid-like) polygons and assesses the intensity of clustering with increasing distance to select an optimal scale of analysis, producing two statistics from the Getis-Ord Gi* test: the *p*-value and the Z-score. The null hypothesis for this test is that mortality events are randomly distributed. This hypothesis can be rejected or accepted based on the Z-score and *p*-values. If the Z-score is closer to zero, it implies that there is a random distribution of spatial events; for statistically significant positive Z-scores, the larger the Z-score is, the greater the clustering of high values (a significant hotspot); for negative Z-scores, the smaller the Z-score is, the greater the clustering of low values (a significant cold spot) (Getis & Ord 1992).

Marsh deer distribution and abundance before and after the 2015-2016 extreme flood. To assess flood-related changes in the distribution and relative abundance of marsh deer, a presence-absence survey was conducted in the study area before (from October to early December 2015) and after (March 2017) the extreme flood event. The study area was divided into a 6 x 6 km grid, and 15 of these grid cells were selected for surveys during both periods based on accessibility and habitat availability for marsh deer. In each grid cell, two of the authors (DV and BVL), who had >15 years of experience identifying marsh deer signs, walked 100-m long transects randomly selected along dirt roads, embankments, and watercourse borders, recording direct observations, footprints, and feces of marsh deer. In addition, the presence of dog and cattle sign, and the dominant habitat type (willow, poplar, pasture), were recorded in each transect as covariates that may affect the presence of marsh deer. An average of 14 and 12 100-m transects were sampled per grid cell, totaling 212 and 185 transects sampled in 2015 and 2017, respectively. The lack of sign of marsh deer, dog, and cattle were considered absences, although we recognize that sign detection was less than perfect. Due to the relative homogeneity of our sample sites, we assumed that the bias in our sampling was consistent across sites.

Generalized linear mixed models (GLMMs) with a binomial distribution were used to assess the presence/absence of marsh deer (response variable) before and after extreme flooding (year) in relation to habitat type (willow, poplar, and pastures) and cattle and dog presence, using the sampled grid cell as a random effect. GLMMs were implemented with "lme4" package (Bates et al. 2015) and model fit was evaluated based on scaled residuals using the DHARMa package (Hartig 2016) in R 4.0.3. The significance level used for the GLMM was set at $p < 0.05$. To graphically assess flood-related changes in marsh deer distribution patterns, an index of minimum relative abundance (MRAI) per grid cell was estimated as the number of transects with marsh deer presence divided by the total number of transects surveyed per grid cell. This approach recognizes that our ability to detect marsh deer may have been imperfect and that our detections represent the minimum number of individuals present. A paired *t*-test was used to compare the mean values of MRAIs before and after the extreme flood.

Marsh deer mortality outside of extreme flooding periods. To collect information on marsh deer mortality during years of "normal" hydrologic conditions, an approach based on reports by key informants and field surveys, similar to that used during the 2015-2016 extreme flood was used in 2018, 2019, and 2021. Local referents from the lower Delta collected and provided marsh deer mortality data, while additional information was obtained by direct communication with other islanders or through social media. In addition, the study area was regularly accessed by the authors (from 2 to >12 times per month) within these years to visit forestry producers or to conduct field research (i.e., camera trapping, drone surveys, capturing and fitting deer with satellite collars, etc.) or educational activities. During these visits, large areas were traversed, including roads, embankments, water courses, tree plantations, and wetlands, among others. Dead marsh deer opportunistically found, or those located due to information provided by residents were revised to determine the cause of death. Finally, official reports of marsh deer deaths produced by local authorities were included in our database. Mortality records from different sources were compared to avoid overestimating mortality (i.e., to avoid more than one report of the same mortality). Because the objective of this survey was simply to assess the minimum number of marsh deer deaths outside of extreme flooding periods, neither statistical analysis nor modeling was conducted with these data. Average monthly mortality rates were estimated to allow comparisons within and outside of extreme flood periods.

RESULTS

Marsh deer mortality

During the 2015-2016 extreme flood, we recorded 142 marsh deer mortalities over six months, 13 of them during field surveys and 129 through informants (**Table** 1). Pooling both data sources, poaching accounted for 86.6% (n = 123) of the total deaths. Eighty-two poached marsh deer were unambiguously identified as adults and 6 deer reported by informants were probably juveniles, while 47 and 31 of the poached deer were identified as males and females, respectively. The age class or sex of the remaining individuals were not identified or reported.

The generalized additive model explained 60% of the total deviance, resulting in an adjusted r^2 of 0.61. The mortality of marsh deer caused by poaching was significantly higher in low-lying areas which corresponded to poplar and willow plantations, and in permanently inundated lands (**Table** 2). Proximity to urban areas and embankments was strongly positively associated ($p < 0.001$) with higher mortality values for marsh deer (**Table** 3; **Fig**. 2), however, mortalities increased again at distances beyond about 20 km from urban areas (**Fig**. 2). Increased proximity to dirt roads was significantly ($p < 0.05$) associated with higher mortality, whereas

Table 1

Sources of mortality and number of dead marsh deer in the 2015-2016 extreme flood in the lower Delta of the Paraná River, Argentina, discriminating by method of data collection.

Cause of mortality	Data from: Field surveys	Data from: Interviews
Poaching	4	118
Poor body condition (disease?)	2	1
Drowning	0	2
Predation by dogs	0	2
Roadkill	0	1
Undetermined	7	5
Total	13	129

mortalities significantly increased ($p < 0.01$) away from watercourses (**Table** 3). Elevation was also positively related to mortality, with significantly ($p < 0.05$) higher numbers of marsh deer deaths occurring in areas of intermediate elevation. Slope, aspect, and the percent of the flooded area at the peak of the flood did not affect marsh deer mortality (**Table** 3; **Fig**. 2).

The optimized hotspot analysis identified two areas with high spatial clustering of marsh deer mortality (i.e., hotspots, with $2.21 \leq Z \leq 3.61$) occurring toward the west-southwest of the study area (**Fig**. 1b). The largest of these clusters ("mortality hotspot 1") made up of 18 significant subdivisions, including five clustered subdivisions with high (99%) confidence surrounded by 13 clustered subdivisions at the 95% confidence level. This mortality hotspot accounted for 63 mortality records and is characterized by large tree plantations of private companies and a small patch (c. 6.7 km^2) of semi-natural vegetation located on riparian lowlands surrounded by an urban area. The other cluster ("mortality hotspot 2"), including two subdivisions at the 99% confidence level and one at the 95% confidence level, was located in tree plantations to the north of mortality hotspot 1.

Marsh deer distribution and abundance before and after the 2015-2016 extreme flood

The probability of marsh deer occurrence was significantly greater before the 2015-2016 flood ($p = 0.039$; **Table** 4) and the presence of cattle and pastures had significant negative effects. Concurrently, marsh deer occurrence was positively associated with willow and poplar plantations (**Table** 4).

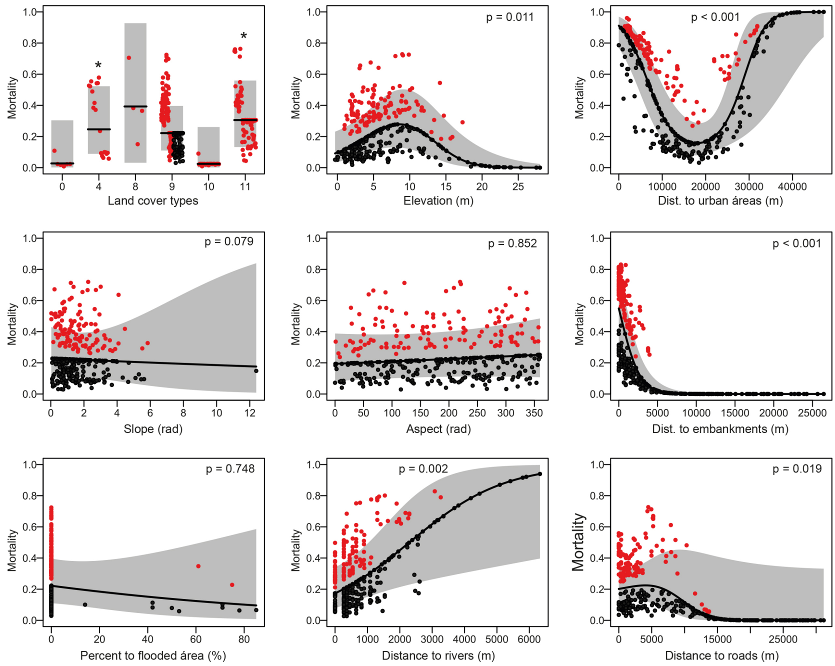

Fig. 2. Partial response of marsh deer poaching mortality to factors (land cover type) and smoothed variables during the 2015-2016 extreme flood in the lower Delta of the Paraná River, Argentina, estimated from the general additive model. The black lines represent the mean partial predicted response for each predictor, the gray shade the 95% confidence intervals around the predicted mean, and the red and black points represent values above and below the estimated relationship, respectively. The estimated effect of each variable on poaching mortality was significant at $p = 0.05$. In the upper left panel (land cover types), an asterisk indicates $p < 0.05$ and categories represented are: (0) permanent water bodies, (4) poplar and willow plantations, (8) marshes with 30%-60% tree cover, (9) marshes with 10%-30% tree cover, (10) grasslands, and (11) permanently flooded lands.

Table 2

Results of the generalized additive model with binomial response for poaching mortality in marsh deer in the 2015-2016 extreme flood in the lower Delta of the Paraná River, Argentina. Summary statistics with statistically significant factors in bold.

	Estimate	SE	*P*
Intercept	**−7.884**	**2.068**	**< 0.001**
Land cover type (poplar and willow plantations)	**3.590**	**1.648**	**0.029**
Land cover type (marshes with 30%-60% tree cover)	3.517	2.287	0.124
Land cover type (marshes with 10%-30% tree cover)	2.462	1.511	0.103
Land cover type (grasslands)	0.531	2.024	0.792
Land cover type (permanently flooded lands)	**3.528**	**1.549**	**0.022**

The average marsh deer MRAI (n = 15 grid cells) exhibited a decreasing trend between before (mean = 0.461; range = 0.067-0.714; median = 0.462) and after (mean = 0.409; range = 0-0.846; median = 0.364) the extreme flood event, although not significantly different ($t = 0.99$; *d. f.* = 14; $p = 0.34$). While 10 of 15 assessed grid cells showed a decrease in their MRAIs after the flood, five grid cells exhibited an increase (**Fig.** 1c). Changes in relative abundance between periods were heterogeneous across the landscape, but the grid cells with the greatest decrease in MRAI were located in the southwest, and partially

Table 3

Observed ranges of covariates considered and results of the generalized additive model with binomial response for poaching mortality in marsh deer during the 2015-2016 extreme flood in the lower Delta of the Paraná River, Argentina. Summary statistics for smooth terms with statistically significant terms in bold. Edf: effective degrees of freedom (values close to 1 indicate a linear partial relationship with the response; see Fig. 2).

	Observed range (min-max)	Edf	χ^2	*P*
Elevation (m)	**−0.32-28.00**	**1.932**	**9.028**	**0.011**
Distance to urban areas (m)	**0.00-47 166.12**	**2.000**	**31.959**	**< 0.001**
Slope (rad)	0.03-12.39	1.788	4.374	0.079
Aspect (rad)	0.00-359.76	1.000	0.035	0.852
Distance to embankments (m)	**0.00-26 447.65**	**1.000**	**20.571**	**< 0.001**
Percent of flooded area (%)	0.00-85.00	1.000	0.103	0.748
Distance to rivers (m)	**0.00-6 328.82**	**1.000**	**9.788**	**0.002**
Distance to roads (m)	**0.00-31 154.51**	**1.736**	**9.596**	**0.019**

Table 4

Results of the generalized linear mixed model with binomial distribution used to assess the presence-absence of marsh deer before and after the 2015-2016 extreme flood in the lower Delta of the Paraná River, Argentina. Statistically significant terms (at the $p < 0.05$ level) are in bold.

	Estimate	SE	*P*
Intercept	0.1239	0.3740	0.740
Year (2017)	**−0.5136**	**0.2485**	**0.039**
Habitat type (willow)	**0.9725**	**0.3297**	**0.003**
Habitat type (poplar)	**0.7193**	**0.3571**	**0.044**
Habitat type (pastures)	**−0.9640**	**0.4167**	**0.021**
Presence of cattle	**−1.6452**	**0.2815**	**< 0.001**
Presence of dogs	−0.4256	0.3050	0.163

overlapping mortality hotspot 1, whereas the grid cell containing mortality hotspot 2 showed a slight increase in its MRAI value after the flood (**Fig**. 1c).

Marsh deer mortality outside extreme flooding periods

We recorded 31 marsh deer deaths in 2018, 38 in 2019, and 52 in 2021, which translated into average rates of 2.58, 3.16, and 4.33 marsh deer deaths per month for 2018, 2019, and 2021, respectively. The average monthly mortality rate recorded from December 2015 to June 2016 during extreme flooding (20.29 marsh deer deaths per month) represents a 469%-786% increase in the average monthly mortality rate between periods within and outside of extreme flooding. Considering only poaching-related mortality (22 cases in 2018, 35 in 2019, and 37 in 2021), the average monthly mortality rate recorded during extreme floods (17.57 poached marsh deer per month) represents an inter-period increment of 570%-960% in this rate due to poaching.

DISCUSSION

Extreme flood periods are critical moments for the dynamics of the marsh deer population inhabiting the lower Delta of the Paraná River. The occurrence of the extreme 2015-2016 flood in this wetland increased the poaching mortality of marsh deer, with deer mortality significantly greater in proximity to urban areas, embankments, and dirt roads, while mortality from poaching was greater in poplar and willow plantations and permanently inundated lands. The association with willow and poplar plantations was expected because they provide adequate habitat for marsh deer in the lower Delta and support the majority of the marsh deer population in our study area (Varela 2003; Fracassi & Somma 2010; Pereira et al. 2023). The strong association of mortalities with embankments built for plantation forestry was also expected as terrestrial species survive in flooded landscapes by moving onto islands formed by embankments (Yeager & Anderson 1944; Wuczynski & Jakubiec 2013) and are subsequently more easily encountered by poachers. Concurrently, since marsh deer and other animals (including cattle) are usually obligated to share these restricted spaces, increased malnutrition and exposure to disease may also occur (Orozco et al. 2020). To the best of our knowledge, this is the first study to show how the co-occurrence of extreme flooding and poaching, along with the potential synergistic effects of food scarcity and disease, can turn embankments into attractive population sinks. However, we recognize that our data may be biased toward areas where our informants had better access, to sources of mortality more easily detected by informants (i.e., poaching), or that some local people were hesitant to talk about illegal activities, so our results may underestimate actual poaching numbers.

The positive relationship between marsh deer mortalities and proximity to urban areas may be attributed to migration to Pampean grasslands not normally occupied during ordinary hydrological conditions. Although this behavioral response has been documented historically (Lynch-Arribálzaga 1878; Garra 1955), these refuge areas have been rapidly urbanized in the last decades. This increased proximity to human populations results in greater levels of poaching, as well as threats from free-ranging domestic dogs, fire, and vehicle collisions, resulting in these refuge areas increasingly acting as population sinks. Similarly, increased mortality of marsh deer occurred in low-lying commercial plantations located near urban areas because these plantations were easily accessible through navigable channels or dirt roads. Supporting the relationship between poaching mortality and proximity to the human population, the hotspot analysis showed that mortalities were concentrated in proximity to urban areas with easy access via water or dirt roads.

A higher mortality rate near human settlements is a pattern often observed in other studies of poached ungulates (e.g., Abrahams et al. 2017; Wilkie et al. 2000; Kumar et al. 2021). However, in our system, the mortality of marsh deer also increased at distances > 20 km from urban areas, which we attribute to the activities of poachers who usually target these areas because they are infrequently patrolled by law enforcement while avoiding areas where their activities can be detected (e.g., Milner-Gulland & Leader-Williams 1992). During 2015-2016 flood, poachers appear to have maximized their hunting success by targeting areas far from urban centers with a higher perceived marsh deer abundance and lower frequency of anti-poaching activities. Poaching is likely the most important factor in the decline of the largest terrestrial herbivores in much of the developing world (Ripple et al. 2015), with the development of effective conservation solutions challenging as poaching is driven by a confluence of economic, social, and cultural factors (Challender & Macmillan 2014; Travers et al. 2019). Reducing the threat of poaching to the marsh deer population in the lower Delta is subject to all of these challenges. Therefore, our results have important applications as they can be used to prioritize anti-poaching efforts, especially for future extreme flooding events.

We found that flood-related mortality of marsh deer significantly decreased the occurrence of the species in the study area after the flood, although the signs-based MRAI method showed a nonsignificant trend. However, the latter result may be due to the low statistical power of this approach to detect population changes (Gibbs 2000). Interestingly, the MRAI approach indicated a spatially heterogeneous response of the marsh deer population to the flooding, with local migrations offsetting some of the negative effects of this extreme event. The high mobility of the marsh deer could explain the slight increment in relative abundance recorded after the flood in the area of mortality hotspot 2. In contrast, the subpopulation of marsh deer in the areas located in or near mortality hotspot 1 was unable to recover its numbers less than one year after the extreme flood, probably due to the large number of individuals poached during the flood.

Understanding how increasing human population density, climate change, and hunting/poaching affect large herbivores has been highlighted as a critical research step to conserving the world´s largest herbivores (Ripple et al. 2015). This is especially important for species living in human-dominated landscapes that are obligated to migrate in response to periodic hydrologic events. Northeastern Argentina is one of the regions in South America most exposed to the risk of flood-related disasters (Prieto 2007), with an increase in the frequency of extreme ENSO events and related flood risk expected due to global climate change (Milly et al. 2002; Hirabayashi et al. 2013; Cai et al. 2017). Consequently, our findings show that the direct and indirect effects of increased extreme floods are likely an important threat to the conservation of marsh deer in the lower Delta. Because climate change is expected to increase the global frequency and magnitude of extreme flood events, our study provides valuable information for mitigating the negative synergistic effects of extreme flooding and poaching on the marsh deer in the lower Delta of the Paraná River and range-wide, as well as for global wildlife populations exposed to periodic extreme floods.

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