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ORIGINAL RESEARCH

Activity patterns of the marsh deer: Effects of proxies of human movement, cattle presence, and moon phases on its behavior

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Abstract

Activity is an important aspect of animal behavior. Intrinsic and extrinsic factors can shape species activity patterns, which can alter and reshape several ecological aspects of the species. Human disturbance is known to modify the activity patterns of various species. The Marsh deer (*Blastocerus dichotomus*) is the largest Neotropical cervid, and has its southernmost distribution located in the wetlands of the lower Delta of the Paraná river, an area characterized by forestry plantations. We studied how the activity patterns of the marsh deer are affected by proxies of human movement, cattle presence, and moon phases in Argentina. We found that marsh deer presented activity peaks during crepuscular hours and moderate levels of activity during the entire night period. The majority of the independent camera-trapping events of marsh deer occurred during the first quarter and last quarter phases, and the species was more active on sites far from rivers, which could infer an avoidance of human disturbances. In order to comprehend more deeply the variable effects on the activity patterns of marsh deer in this area, further analyses are needed, particularly using movement data of marked individuals.

Introduction

Animal activity is an important dimension of animal behavior. Daily activity patterns might be seen as ‘adaptive sequences of daily routines that meet the time structure of the environment, shaped by evolution, but additionally fine-tuned by flexible responses to the actual state of the environment’ (cf. Halle, 2000). Environmental and human-related stressors (i.e., intrinsic or extrinsic factors that obligate individuals to adjust behavior) can alter activity patterns and reshape a wide range of ecological aspects such as reproduction, feeding, or community interactions (e.g., Killen et al., 2013; Stankowich, 2008; Wang et al., 2015). In a recent review of the effects of humans on daily patterns of wildlife activity, Gaynor et al. (2018) estimated that animals have increased their nocturnality by an average factor of 1.36 in response to human disturbance. Although this temporal avoidance may facilitate human-wildlife coexistence, such responses can result in marked shifts away from natural patterns of activity (Gaynor et al., 2018). Due to the possible consequences of these adjustments, understanding how these stressors affect animal activity in different contexts is an important behavioral research topic.

Globally, large mammalian herbivores (body mass ≥ 100 kg) are facing dramatic population declines and range contractions, mainly due to hunting, land-use change, and resource depression by livestock (Ripple et al., 2016). Identifying the different ways in which habitat transformation, rising livestock densities, and hunting, as well as different combinations of these factors, affect large herbivores could have important conservation implications to understand and eventually reverse these negative trends. Shifts in daily activity patterns of ungulates in response to human-related stressors have been described, including human recreation (Reilly et al., 2017), hunting pressure (e.g., Di Bitetti et al., 2008; Espinosa & Salvador, 2017; Kilgo et al., 1998), coexistence with cattle (Di Bitetti et al., 2020; Nanni, 2015; Pudyatmoko, 2017), and domestic dog presence (Zapata-Ríos & Branch, 2016).

On the other hand, moonlight is also an (abiotic) determinant of the nocturnal activity patterns of ungulates (e.g., Brown et al., 2011; Walther, 1973). Moon brightness can affect visual, auditory, and olfactory conditions at night (Cherry & Barton, 2017; Ruzicka & Conover, 2011) and the ability of predators and prey to detect each other (D'Angelo et al., 2008; Ditchkoff, 2011). For example, bright moonlight provides the best hunting conditions for wolves (*Canis lupus*) as their prey are more easily detectable (i.e., Theuerkauf et al., 2003). When predators are present, ungulates tend to assign more time to vigilance (e.g., Childress & Lung, 2003), altering the time allocated for other activities (i.e., feeding) and thus the overall activity budget (Creel et al., 2005). Similar behavioral responses have also been observed for species subjected to hunting/poaching: hunting pressure can trigger indirect non-lethal effects on the behavior of animals, modifying their activity rhythms or habitat use at night (e.g., Benhaiem et al., 2008; Espinosa & Salvador, 2017; Jeppesen, 1987).

Marsh deer (*Blastocerus dichotomus*, Fig. 1), the largest Neotropical cervid (up to 150 kg in body mass), are distributed from southern Amazonia to central Argentina (Duarte & González, 2010). The species has morphological and ecological adaptations to live in wetlands and riparian habitats (Piovezan et al., 2010). As a result of poaching and habitat loss due to agricultural activities, marsh deer populations are declining throughout their range and the species has been globally categorized as 'Vulnerable' (Duarte et al., 2016). The southernmost population of this deer is found in the lower Delta of the Paraná River, one of the largest wetlands in Argentina (Malvárez, 1999), where the species has been categorized as 'Endangered' (Pereira et al., 2019). Commercial tree plantations of poplar (*Populus* spp.) and willow (*Salix* spp.) are currently the main production activity in this wetland (MAGyP, 2011), but a recent expansion in cattle ranching practices has occurred, increasing cattle numbers from 160 000 heads in 1997 to 1 500 000 heads in 2007 (Quintana et al., 2014). To accommodate these developing production activities, a large-scale replacement of native vegetation has occurred, and one-third of the freshwater marshes (1600 km^2) has been replaced by pastures (70%) and forestry (18%), between 1999 and 2013 (Sica et al., 2016). Although no natural predators of marsh deer are present in the lower Delta, the species is subjected to an intensive poaching pressure (Pereira et al., 2019). The large-scale habitat conversion, the increasing cattle numbers, and the widespread poaching pressure that the species is facing in this wetland may have affected its behavior, but neither any study of its daily activity patterns nor any assessments of temporal responses by this ungulate to these stressors have been carried out.

In this work, the daily activity patterns of the marsh deer in the human-dominated landscape of the lower Delta of the Paraná River are described, exploring the influences of indirect human disturbances and moon phases on the temporal patterns of the species. Specifically, we proposed to: (1) analyze the overall daily activity patterns of this marsh deer population through camera trapping; (2) examine the potential effects of cattle presence and proxies of human movement on the daily activity patterns of the marsh deer; and (3) assess the effects of moon phases on the activity levels of this species.

Materials and methods

Study area

The lower Delta of the Paraná River (33°48′ to 34°26′S, 59°00′ to 58°31′W) is located in Argentina, at the end of the Paraná River and in the upper portion of the Rio de la Plata estuary (Malvárez, 1999; Fig. 1). The region has a sub-humid temperate climate with a mean annual temperature between 16.7°C and 18°C and a mean annual precipitation of 1000 mm (Instituto Nacional de Tecnología Agropecuaria; http://

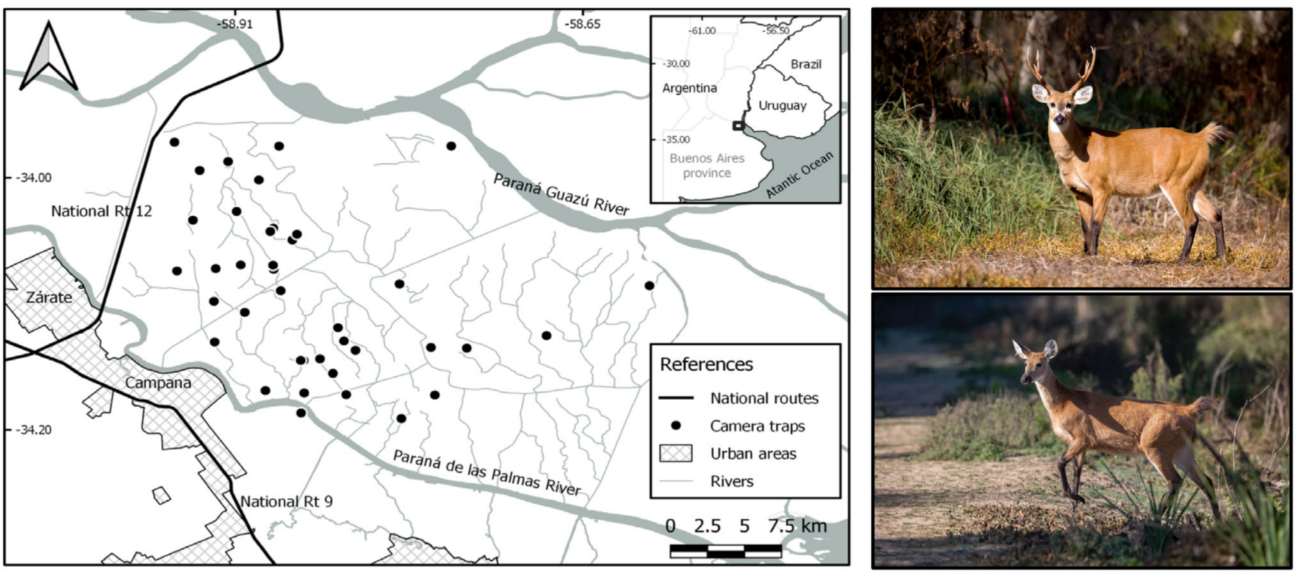

Figure 1 Study area location and camera trap sites distributed in the lower Delta of Paraná River. Pictures of the species in the study area: above an adult male, below an adult female. Pictures kindly provided by Esteban Argerich.

climayagua.inta.gob.ar/estadisticas_de_precipitaciones). The islands of the lower Delta used to have permanently flooded lowlands with bulrush marshes in their interior fringed by natural levees where riparian forests were settled (Burkart, 1957; Kandus et al., 2006). Currently, the original landscape is highly transformed due to anthropogenic activities, mainly by forestry activity (Sica et al., 2016). Specifically, this study was mainly carried out in an area of c. 500 km^2 in a so-called 'forestry nucleus' which is located within the insular portion of the lower Delta (Fig. 1). The forestry nucleus is the area with the highest concentration of tree plantations and embankments of the lower Delta (Fracassi et al., 2014). Cattle raising and associated water management practices (i.e., embankments, ditches, and channels; Minotti, 2019; Sica et al., 2016) are secondary activities developed in this area. A network of dirt roads, including a few public main roads and several minor roads and tracks, located inside the proprieties, connect production lands across the landscape. Ferry boats are used to connect dirt road sections where rivers and channels occur. Rivers and main channels are also used by local people to travel by boat all year round.

Data collection

Camera traps are becoming increasingly popular instruments to address behavioral questions (Burton et al., 2015; Caravaggi et al., 2017; Frey et al., 2017). Camera trap surveys were conducted during the years of 2014 (from January to March), 2015 (from January to March and from November to December), 2017 (from June to September), and 2018 (from February to December), focusing on an area of ca. 580 km^2 (minimum convex polygon of the area encompassed by the whole camera-trapping stations set) under intensive forestry management. The primary objective of these surveys was to estimate population attributes and behavior of the marsh deer and other large and medium-sized mammals that inhabit this region. The sites included in the activity pattern analyses were located in forestry plantations (e.g., poplar, willow; Fracassi et al., 2014). Some sites (i.e., 6 sites) presented presence of cattle (fattening phase).

Each sampling station consisted of a single camera-trap set (Bushnell Trophy Cam series, Bushnell Corporation, Kansas, USA) ca. 50 cm from the ground, active 24 h, not baited and with no particular orientation. The ground in front of the cameras was cleaned of debris and vegetation. The cameras were programmed to take three photographs and a 30-s film at every triggering event (with no delay between events). To prevent prolonged malfunctioning, the cameras were checked every 15–20 days. Successive photographs of the same individual in a sampling station were defined as independent events (henceforward 'marsh deer event/second') when separated by more than 1 h (henceforth '1-h criteria'). Between the sites there was at least 2 km of distance.

A total of 42 camera trapping stations were installed during the whole survey (Fig. 1). On average, each camera trapping station was active for 60.2 ± 31.6 (SD) consecutive days (range = 6–136), leading to an overall effort of 2693 camera trapping days (Table 1).

Table 1 Sampling design and distribution of independent marsh deer activity events obtained in the lower Delta of the Paraná river, 2014–2018

Year	No. of camera trapping stations	Camera trapping effort (traps/day)	Average minimum distance between adjacent cameras (km ± SD)	No. of independents marsh deer events
2014	11	670	2.9 ± 1.9	46
2015	8	253	2.6 ± 1.1	114
2017	9	557	4.9 ± 2.1	76
2018	14	1213	5.5 ± 2.7	142
Total	42	2693		378

Data analysis

Marsh deer activity pattern

Camera-trap photo management and the creation of the database of marsh deer records were conducted using Wild.ID v1.0.1 (TEAM- https://www.wildlifeinsights.org/team-network). Activity was estimated from the time and date imprinted on the photographs. Due to the relatively low number of records obtained during each sampling period (Table 1), neither inter-annual nor seasonal analysis of activity patterns was attempted. The marsh deer events were pooled and the daily activity patterns were estimated by applying the kernel density method with the *Overlap* package for R software (Meredith & Ridout, 2014; R Core Team, 2017). We classified the marsh deer activity during four phases: day, night, dusk, and dawn (the time information for each phase was extracted from the online database https://www.sunrise-and-sunset.com). To reflect seasonal changes in dusk and dawn periods due to seasonal changes in day length, these periods were considered to start an hour before and to end an hour after the average sunrise and sunset times, respectively. In order to understand if there was a preference or avoidance of a certain day phase by marsh deer, we applied a Jacob Index (Jacobs, 1974) according to the formula: $D = (r-p)/(r + p-2rp)$, where r is the proportion of the day 'used' (number of marsh deer events per day phase/total marsh deer events) and p the proportion of the day 'available' (duration, in hours, of the day phase/total length of a day). The Jacob Index varies between −1 (strong avoidance) and 1 (strong preference; Jacobs, 1974).

Modeling the activity pattern of marsh deer with proxies of human movement (rivers and roads) and cattle presence

In order to understand if human movement could affect marsh deer activity, we analyzed the effects on its behavior of the main transportation features in the study area (rivers and roads as proxies of 'human movement'). Per each camera trap site, we calculated the minimum distance (in meters) from the site to the closest river with QGis software (QGIS Development Team, 2020). In order to understand if the roads were affecting the activity patterns of marsh deer, we calculated, for each site, a buffer of 1-km radius (corresponding to an area of 3.14 km^2, or the minimum value of an estimated home range in this study area; Pereira et al., 2019), inside of which we extracted the roads' total length, in meters. These processes were all completed in QGis (QGIS Development Team, 2020). We defined presence/absence of cattle in the sites, by considering as 'presence' any site with an independent camera-trap event (i.e., 1-h criteria) of cattle.

In order to comprehend if the marsh deer activity pattern was significantly affected by a proxy of 'human movement', by a particularly day period or by the presence of cattle, we applied a Generalized Linear Model (Gaussian Family). We set as response variable the rate of marsh deer events (i.e., number of independent camera-trapping events/site effort) per site, and as explanatory variables (1) the length of roads per buffer (continuous variable), (2) the distance to the closest river from the sites (continuous variable), (3) the presence/absence of cattle in the sites (binary variable) and (4) the day phase (categorical variable). Since all the sites were distributed in similar habitat (i.e., forestry plantation), we did not include a habitat variable in the model. We applied a Kendall correlation analysis in order to analyze potential correlation between the continuous variables, after which we scaled the continuous variables. For these analyses, we used the packages lme4, MuMIn, and MASS from R Software (R Core Team, 2017).

Cattle activity pattern

The cattle events were collected from the same trapping sessions and design described in the section 'Data collection'. In order to understand the effect of the presence of cattle in the sites (n = 6) included in the model previously described, we estimated the activity pattern of cattle applying the kernel density method with the *Overlap* package for R software (Meredith & Ridout, 2014; R Core Team, 2017). We also overlapped the activity pattern of cattle and marsh deer by using the *Overlap* package for R software (Meredith & Ridout, 2014; R Core Team, 2017) and we estimated the overlap coefficient Dath4 (range 0–100%), which is recommended for small samples (Meredith & Ridout, 2014). For this, we included 57 independent camera-trapping events of cattle (1-h criteria) and 56 independent events of marsh deer distributed in the 6 sites where these species co-occurred.

Moon phases and marsh deer activity

To evaluate the effects of moonlight on the nocturnal activity of marsh deer, eight moon phases were considered: full moon, waxing gibbous/waning gibbous, waning crescent/waxing crescent, first and last quarter, and new moon (Appendix S1). We consider for these analyses the moon phase at 12:00 PM. We were not able to consider cloud cover in these analyses since the data was not available for the study area. We extracted, per each event (total nocturnal events = 127), the moon phase with the function lunar phase of the package *lunar* of the R software (R Core Team, 2017).

Results

Marsh deer activity

Overall, 378 independent camera-trapping records of marsh deer were obtained and included in this study. Marsh deer activity events were almost evenly distributed between day (39.4%) and night (38.3%), and between dawn (10.1%) and dusk phases (12.2%). Whereas activity records were homogeneously distributed throughout the nocturnal period, diurnal activity showed a marked peak toward the morning hours (Fig. 2). A second daily activity peak occurred during the sunset (Fig. 2). The Jacob index did not present a marked preference or avoidance toward a particular day phase (Fig. 3).

Modeling the activity pattern of marsh deer with proxies of human movement and cattle presence

The model with all the variables showed that marsh deer activity pattern was significantly affected by the 'distance to the closest river' (Table 2; $P < 0.05$), meaning that marsh deer were more active in the sites far from rivers, and also were marginally affected by the ''night period' (Table 2; $P = 0.06$).

Cattle activity pattern

Overall, cattle presented a diurnal activity pattern (Fig. 4). These animals concentrated their activity after the sunrise and before sunset in those sites where they were co-occurring with marsh deer (Fig. 4). The overlap coefficient was of 58%, and the majority of the overlapped activity occurred during the morning hours (Fig. 4).

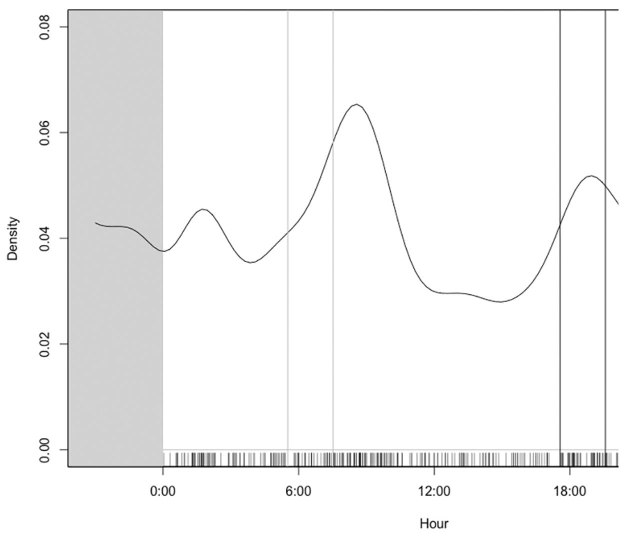

Figure 2 Activity pattern of marsh deer in the lower Delta of the Paraná river. The gray vertical lines indicate the average sunrise hours between the sampled years, and the black vertical lines indicate the average sunset hours between the sampled years.

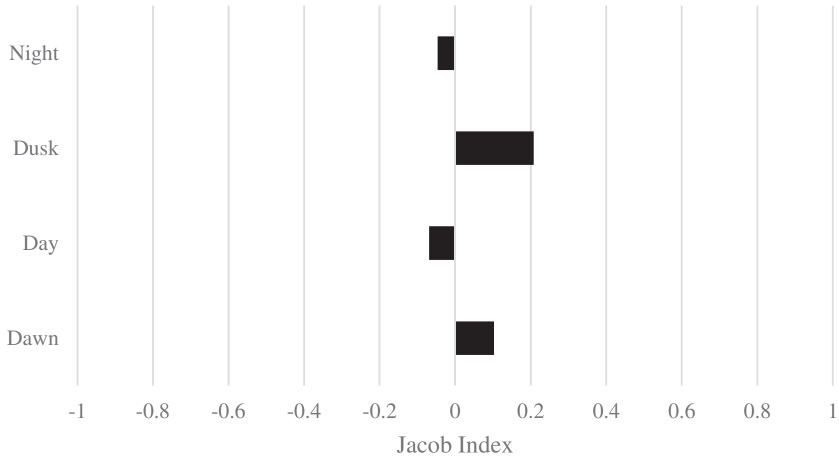

Figure 3 Jacob index applied to illustrate potential selection or avoidance of marsh deer toward a day phase.

Table 2 Results of the model applied to estimate the effects of a set of variables on the marsh deer activity pattern in the lower Delta of Paraná river

	Estimate	SE	*Z*-value	*P*-value
(Intercept)	0.04	0.03	1.12	0.26
Length of roads per buffer	0.02	0.01	1.43	0.15
Distance to the closest rivers	0.06	0.01	3.49	<0.05
Presence of cattle	−0.03	0.11	−0.33	0.73
Dusk period	−0.005	0.05	−0.11	0.9
Day period	0.05	0.05	1.13	0.25
Night period	0.09	0.05	1.82	0.06

SE, standard error.

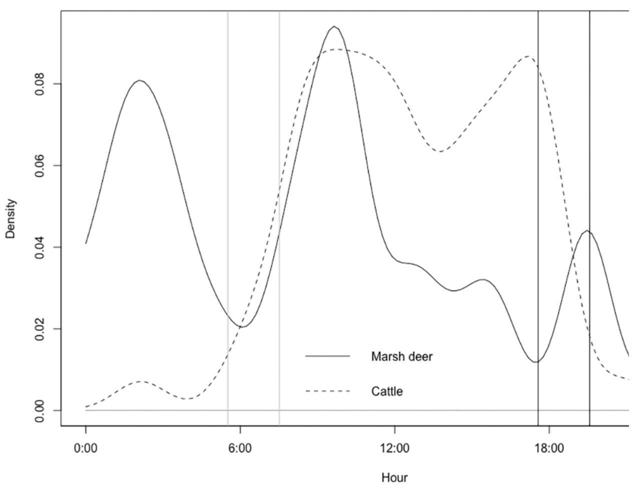

Figure 4 Overlapped activity patterns of cattle and marsh deer in the sites with co-occurrence ($n = 6$). The gray vertical lines indicate the average sunrise hours between the sampled years, and the black vertical lines indicate the average sunset hours between the sampled years.

Moon phases and marsh deer activity

The majority of the independent camera-trapping events of marsh deer occurred during the first quarter (n = 22 events) and last quarter (n = 21 events) phases.

Discussion

Marsh deer activity

The daily activity of marsh deer in the lower Delta of the Paraná River presented a first peak of activity during the early morning and a second peak during the sunset. Scarce information is available on the activity patterns of the species across its distribution. Andriolo et al. (2003) found that deer in the upper Paraná River (Brazil) were more active during the night period, suggesting that this species avoids the hottest temperatures of the daylight hours. Lehndal (2008) also found that marsh deer were mainly nocturnal in the Jataí Ecological Station (Brazil), hypothesizing that environmental temperature and predator pressure were the variables affecting the activity of this ungulate the most. Normally, the activity patterns of ruminants are related to feeding rhythm (Hofmann, 1989). This rhythm is characterized by the morphology of the stomach and digestion physiology, and includes feeding, ruminating and resting behaviors (Hofmann, 1989). Indeed, ruminant species that are morpho-physiologically intermediate (e.g., red deer *Cervus elaphus*) present a bimodal feeding rhythm (Hofmann, 1989). Bimodal activity patterns have been widely reported for other deer species of similar size to the marsh deer (e.g., white-tailed deer *Odocoileus virginianus*, Beier & McCullough, 1990; red deer, Ensing et al., 2014; Sika deer *Cervus nippon*, Ikeda et al., 2015). Environmental temperature could be one factor explaining the bimodal activity of deer species. For example, sika deer tend to decrease its activity with increasing temperatures (Ikeda et al., 2015). Similarly, white-tailed deer activity seems to be negatively affected by temperature, particularly in the autumn (Beier & McCullough, 1990). Marsh deer in our study also showed a bimodal activity pattern and were mostly inactive during the hottest hours of the day, suggesting that temperature could be a potential factor influencing the activity rhythms of this ungulate.

Modeling the activity pattern of marsh deer with proxies of human movement and cattle presence

We found that marsh deer were more active in sites far from rivers (Table 2). Due to the challenging accessibility to the study area, rivers represent one of the main transportation channels for humans. We believe that rivers, for marsh deer, could represent sites with more anthropic disturbance compared with other sites in the landscape (e.g., sites with roads). Although there is no published evidence regarding the use of rivers by hunters in the area, studies in basins have identified rivers as a proxy for hunter accessibility (e.g., De Thoisy et al., 2005). Hunting and fishing in the lower Delta of Paraná river are common activities carried out by local people and 'outsiders' (Cassini & Tunez, 2019). Among the mammals most hunted, two large rodents (capybara *Hydrochoerus hydrochaeris* and coypus *Myocastor coypus*) and the marsh deer were identified (Cassini & Tunez, 2019).

Cattle activity pattern

Temporal (non)interactions between native herbivores and domestic cattle have been the main focus of different studies, particularly with some northern species (e.g., elk and mule deer: Stewart et al., 2002; spotted deer *axis*, swamp deer *Cervus duvaucelii*: Regmi et al., 2020; Italian roe deer *Capreolus italicus*, Gaudiano et al., 2021). Several of such studies report a temporal segregation between deer species and cattle (e.g., elk and mule deer: Stewart et al., 2002; mule deer: Cooper et al., 2008) and most of them relate this with a potential resource partitioning between the species (e.g., Stewart et al., 2002) or a possible displacement of smaller deer species by larger ungulates (e.g., Coe et al., 2004). In the southern hemisphere, Di Bitetti et al. (2020) found that marsh deer used less frequently areas where cattle were present and avoided being simultaneously active with grazing cattle, suggesting that cattle exert interference competition on the marsh deer. Although we can hypothesize that marsh deer in our study area avoided cattle temporally, still in order to deeply comprehend the interactions between this species and the domestic one, it is necessary to complete the analyses of the temporal data with resource partitioning and spatial data of these species in the study area.

Lunar phases

Although no statistical analyses were completed to understand how the moon phases affected marsh deer activity patterns in the area, the species activity was concentrated mainly during the last and first quarter moon phases. During the first quarter phase, the moon is 90° away from the sun in the sky and is half-illuminated (50%) from our point of view. Higher luminosity at night can increase ungulate activity, since, for them, it is easier to detect risk factors (e.g., predators, hunters; Colino-Rabanal et al., 2018); or higher luminosity may also decrease their activity since they can be more detectable to predators (Colino-Rabanal et al., 2018; Gordigiani et al., 2022). Responses to light and darkness in mammals depend largely on optical anatomy and physiology (Beier, 2006). Deer are equipped with formidable night vision capability since they have a high number of rod cells for black and white vision and night vision (Beier, 2006) and present the *tapetum lucidum* which improves vision in low-light conditions (D'Angelo et al., 2008). These anatomical and physiological characteristics may enhance the ability of deer to detect predators (Birgersson et al., 2001; VerCauteren & Pipas, 2003), making nights with more light less risky. Several studies found a correlation between deer activity and brighter nights: mule deer *Odocoileus hemionus* were more active at salt licks on full moon nights (Buss & Harbert, 1950), Kammermeyer (1975) found increased nocturnal movement of white-tailed deer under full moon, Newhouse (1973) observed that white-tailed deer used more open habitat during brighter nights, and Colino-Rabanal et al. (2018) detected an increase in deer-vehicle collisions on full moon nights. On the other hand, Kie et al. (1991) recorded that mule deer, during nights with bright moonlight, fed less and moved this activity to other parts of the day. Also, Goethlich (2020) found that females of white-tailed deer were less active during brighter moon phases during the pre-breeding season than during the breeding and post-breeding seasons, suggesting that inter-seasonal differences could be related to hunting pressure (the hunting season in this study coincided with the breeding and post-breeding seasons). Females may be avoiding those nights with more light because they perceived greater risk to themselves or their fawns from natural and unnatural predators (Goethlich, 2020). Marsh deer in the lower Delta have no natural predators, but the species in heavily poached in the area (Pereira et al., 2019). Official records of marsh deer hunted in the study area (Appendix S2), showed that the individuals were more hunted during the waxing gibbous/waning gibbous phases (41.17%, $n = 7$ hunting events), which correspond to moon illumination between 51% and 90% (see Penteriani et al., 2010). Although hunters may use spotlights to facilitate the detection of marsh deer individuals, one hypothesis is that this species could be avoiding those moon phases with more abundant light in order to be less detectable to humans. Further analyses are required to comprehend and define this potential relation.

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Conflict of interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Competing interests

We disclose any financial or non-financial interests that are directly or indirectly related to the work.

References

Andriolo, A., Da Costa, M. P., Piovezan, U., Torres, H., & Duarte, J. (2003). Activity period of marsh deer (*Blastocerus dichotomus*) monitored by telemetry. *Revista de Etologia*, **5**, 141.

Beier, P. (2006). Effects of artificial night lighting on terrestrial mammals. In C. Rich & T. Longcore (Eds.), *Ecological consequences of artificial night lighting* (pp. 19–42). Island Press.

Beier, P., & McCullough, D. R. (1990). Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs*, **109**, 3–51.

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. M., Morellet, N., & Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour*, **76**, 611–618.

Birgersson, J., Alm, U., & Forkman, B. (2001). Colour vision in fallow deer: A behavioural study. *Animal Behaviour*, **61**, 367–371.

Brown, B., Bryntesson, F., Cooper, S., Nyholm, B., Robertson, D., Bedford, A., Hendricks, D., Klippenstein, L., & Potapov, E. (2011). Moonlight and suburban white-tailed deer movements. *Bulletin of the New Jersey Academy of Science*, **56**, 1–4.

Burkart, A. (1957). Ojeada sinóptica sobre: La vegetación del Delta del Río Paraná. *Darwin*, **11**, 457–561.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, **52**, 675–685.

Buss, I. O., & Harbert, F. H. (1950). Relation of moon phases to the occurrence of mule deer at a Washington salt lick. *Journal of Mammalogy*, **31**, 426–429.

Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M., Haswell, P. M., Hayward, M. W., Rowcliffe, M., & Wood, M. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, **3**, 109–122.

Cassini, M. H., & Tunez, J. I. (2019). Situación ambiental del Bajo Delta del Paraná:¿ Qué opinan los pobladores? *Austral Ecology*, **29**, 296–305.

Cherry, M. J., & Barton, B. T. (2017). Effects of wind on predator-prey interactions. *Food Webs*, **13**, 92–97.

Childress, M. J., & Lung, M. A. (2003). Predation risk, gender and the group size effect: Does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, **66**, 389–398.

Coe, P. K., Johnson, B. K., Stewart, K. M., & Kie, J. G. (2004). *Spatial and temporal interactions of elk, mule deer, and cattle*. Transactions of the 69th North American Wildlife and Natural Resources Conference: 656-669.

Colino-Rabanal, V. J., Langen, T. A., Peris, S. J., & Lizana, M. (2018). Ungulate: Vehicle collision rates are associated with the phase of the moon. *Biodiversity and Conservation*, **27**, 681–694.

Cooper, S. M., Perotto-Baldivieso, H. L., Owens, M. K., Meek, M. G., & Figueroa-Pagan, M. (2008). Distribution and interaction of white-tailed deer and cattle in a semi-arid grazing system. *Agriculture, Ecosystems and Environment*, **127**, 85–92.

Creel, S., Jr Winnie, J., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, **86**, 3387–3397.

D'Angelo, G. J., Glasser, A., Wendt, M., Williams, G. A., Osborn, D. A., Gallagher, G. R., Warren, R. J., Miller, K. V., & Pardue, M. T. (2008). Visual specialization of an herbivore prey species, the white-tailed deer. *Canadian Journal of Zoology*, **86**, 735–743.

De Thoisy, B., Renoux, F., & Julliot, C. (2005). Hunting in northern French Guiana and its impact on primate communities. *Oryx*, **39**, 149–157.

Di Bitetti, M. S., Iezzi, M. E., Cruz, P., Varela, D., & De Angelo, C. (2020). Effects of cattle on habitat use and diel activity of large native herbivores in a south American rangeland. *Journal for Nature Conservation*, **58**, 125900.

Di Bitetti, M. S., Paviolo, A., Ferrari, C. A., De Angelo, C., & Di Blanco, Y. (2008). Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica*, **40**, 636–645.

Ditchkoff, S. S. (2011). Anatomy and physiology. In D. G. Hewitt (Ed.), *Biology and management of white-tailed deer* (pp. 43–74). CRC Press.

Duarte, J. M. B., & González, S. (Eds.). (2010). *Neotropical cervidology: Biology and medicine of Latin American deer* (p. 393). Funep/IUCN.

Duarte, J. M. B., Varela, D., Piovezan, U., Beccaceci, M. D., & Garcia, J. E. (2016). *Blastocerus dichotomus*. The IUCN Red List of Threatened Species 2016: e.T2828A22160916. https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T2828A22160916.en

Ensing, E. P., Ciuti, S., de Wijs, F. A., Lentferink, D. H., ten Hoedt, A., Boyce, M. S., & Hut, R. A. (2014). GPS based daily activity patterns in European red deer and north American elk (*Cervus elaphus*): Indication for a weak circadian clock in ungulates. *PLoS One*, **9**, e106997.

Espinosa, S., & Salvador, J. (2017). Hunters landscape accessibility and daily activity of ungulates in Yasuní biosphere reserve, Ecuador. *Therya*, **8**, 45–52.

Fracassi, N., Quintana, R. D., Pereira, J. A., Mujica, G., & Landó, R. (2014). *Estrategias de Conservación de la Biodiversidad en Plantaciones Forestales de Salicáceas del Bajo Delta del Paraná* (1ra ed., p. 56). INTA.

Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation*, **3**, 123–132.

Gaudiano, L., Pucciarelli, L., & Mori, E. (2021). Livestock grazing affects movements and activity pattern of Italian roe deer in southern Italy. *European Journal of Wildlife Research*, **67**, 1–8.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, **360**, 1232–1235.

Goethlich, J. (2020). *Effects of abiotic factors on white-tailed deer activity in South Carolina*. Master thesis. Auburn University, Alabama, US, 134.

Gordigiani, L., Viviano, A., Brivio, F., Grignolio, S., Lazzeri, L., Marcon, A., & Mori, E. (2022). Carried away by a moonlight shadow: Activity of wild boar in relation to nocturnal light intensity. *Mammal Research*, **67**, 39–49.

Halle, S. (2000). Ecological relevance of daily activity patterns. In S. Halle & N. C. Stensteth (Eds.), *Activity patterns in small mammals* (pp. 67–90). Springer.

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, **78**, 443–457.

Ikeda, T., Takahashi, H., Yoshida, T., Igota, H., Matsuura, Y., Takeshita, K., & Kaji, K. (2015). Seasonal variation of activity pattern in sika deer (*Cervus nippon*) as assessed by camera trap survey. *Mammal Study*, **40**, 199–205.

Jacobs, J. (1974). Quantitative measurement of food selection. *Oecologia*, **14**, 413–417.

Jeppesen, J. L. (1987). Impact of human disturbance on home range, movements and activity of red deer (*Cervus elaphus*) in a Danish environment. *Danish Review of Game Biology*, **13**, 1–38.

Kammermeyer, K. E. (1975). *Movement-ecology of white-tailed deer in relation to a refuge and a 371 hunted area*. M.S. Thesis, University of Georgia, Athens, Georgia, USA.

Kandus, P., Quintana, R. D., & Bó, R. F. (2006). *Patrones de paisaje y biodiversidad del Bajo Delta del Río Paraná. Mapa de ambientes (patterns of landscape and biodiversity of the lower Delta of the Paraná River. Map of environments)* (1st ed.). Pablo Casamajor.

Kie, J. G., Evans, C. J., Loft, E. R., & Menke, J. W. (1991). Foraging behavior by mule deer: The influence of cattle grazing. *Journal of Wildlife Management*, **55**, 665–674.

Kilgo, J. C., Labisky, R. F., & Fritzen, D. E. (1998). Influences of hunting on the behavior of white-tailed deer: Implications for conservation of the Florida panther. *Conservation Biology*, **12**, 1359–1364.

Killen, S. S., Marras, S., Metcalfe, N. B., McKenzie, D. J., & Domenici, P. (2013). Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology & Evolution*, **28**, 651–658.

Lehndal, L. (2008). *Activity patterns, diurnal and nocturnal behaviour of the marsh deer (Blastocerus dichotomus*) in the Jataí Ecological Station, Brazil. MSc thesis, University of Uppsala, Sweden, 28.

MAGyP. Ministerio de Agricultura, Ganadería y Pesca (República Argentina). (2011). *Programa de servicios agrícolas provinciales. Proyecto desarrollo sustentable del Delta Bonaerense. Anexo VI. Buenos Aires*. Estudio de Impacto Ambiental y Social. 303.

Malvárez, A. I. (1999). El Delta Del Rio Paraná como mosaico de humedales. In A. I. Malvárez (Ed.), *Tópicos sobre humedales subtropicales y templados de Sudamérica* (pp. 32–50). MAB-ORCYT.

Meredith, M., & Ridout, M. (2014). *Overlap: Estimates of coefficient of overlapping for animal activity patterns R package version 0.2.3. Accesible en*. https://cran.r-project.org

Minotti, P. (2019). *Actualización y profundización del mapa de endicamientos y terraplenes de la región del Delta del Paraná*. Programa Corredor Azul. Fundación Humedales/ Wetlands International.

Nanni, A. S. (2015). Dissimilar responses of the gray brocket deer (*Mazama gouazoubira*), crab-eating fox (*Cerdocyon thous*) and pampas fox (*Lycalopex gymnocercus*) to livestock frequency in subtropical forests of NW Argentina. *Mammalian Biology*, **80**, 260–264.

Newhouse, S. J. (1973). Effects of weather on behavior of white-tailed deer of the George Reserve. *Michigan*. Master thesis. University of Michigan, Michigan, US, 308.

Penteriani, V., Delgado, M. D. M., Campioni, L., & Lourenco, R. (2010). Moonlight makes owls more chatty. *PLoS One*, **5** (1), e8696.

Pereira, J. A., Varela, D., Aprile, G., Cirignoli, S., Orozco, M. M., Lartigau, B., De Angelo, C., & Giraudo, A. R. (2019). *Blastocerus dichotomus*. In Sayds–Sarem (Ed.), *Categorización 2019 de los mamíferos de Argentina según su riesgo de extinción*. Lista Roja de los mamíferos de Argentina Versión digital: http://cma.sarem.org.ar

Piovezan, U., Tiepolo, L. M., Tomas, W. M., Duarte, J. B., Varela, D., & Marinho-Filho, J. S. (2010). Marsh deer *Blastocerus dichotomus* (Illiger 1815). In J. M. B. Duarte & S. Gonzalez (Eds.), *Neotropical Cervidolgy–Biology and Medicine of Latin American Deer* Vol 8 (pp. 66–76). FUNEP-IUCN.

Pudyatmoko, S. (2017). Free-ranging livestock influence species richness, occupancy, and daily behaviour of wild mammalian species in Baluran National Park, Indonesia. *Mammalian Biology*, **86**, 33–41.

QGIS Development Team. (2020). *QGIS geographic information system*. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Quintana, R. D., Bó, R. F., Astrada, E., & Reeves, C. (2014). *Lineamientos Para una Ganadería Ambientalmente Sustentable en el Delta del Paraná (guidelines for* *environmentally sustainable livestock farming in the Delta of the Paraná River)*. Fundación Humedales/Wetlands International LAC.

R Core Team (2017). R: A language and environment for statistical computing. http://www.R-project.org/

Regmi, S., Neupane, B., Dhami, B., Gautam, D., Panthi, S., & Poudel, M. (2020). *Niche breadth and overlap among two sympatric wild ungulates and domestic cattle in Shuklaphanta National Park, Nepal*. Authorea Preprints.

Reilly, M. L., Tobler, M. W., Sonderegger, D. L., & Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biological Conservation*, **207**, 117–126.

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P. A., Macdonald, D. W., Machovina, B., Newsome, T. M., Peres, C. A., Wallach, A. D., Wolf, C., & Young, H. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, **3**, 160498.

Ruzicka, R. E., & Conover, M. R. (2011). Influence of wind and humidity on foraging behavior of olfactory mesopredators. *Canadian Field-Naturalist*, **125**, 132–139.

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.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: A review and meta-analysis. *Biological Conservation*, **141**, 2159–2173.

Stewart, K. M., Bowyer, R. T., Kie, J. G., Cimon, N. J., & Johnson, B. K. (2002). Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. *Journal of Mammalogy*, **83**, 229–244.

Theuerkauf, J., Rouys, S., & Jedrzejewski, W. (2003). Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology*, **83**, 163–167.

VerCauteren, K. C., & Pipas, M. J. (2003). A review of color vision in white-tailed deer. *Wildlife Society Bulletin*, **31**(3), 684–691.

Walther, F. (1973). Round-the-clock activity of Thomson's gazelle (*Gazella thomsoni* Gunther 1884) in the Serengeti National Park. *Zeitschrift für Tierpsychologie*, **32**, 75–105.

Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation*, **190**, 23–33.

Zapata-Ríos, G., & Branch, L. C. (2016). Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. *Biological Conservation*, **193**, 9–16.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Schematic representation of the moon phases considered in this article.

Appendix S2. List records of marsh deer illegal hunting across the lower Delta of Paraná river. Source: Comité Científico Técnico Ciervo de los Pantanos, Organismo Provincial para el Desarrollo Sostenible, unpublished report.