






## NOTE

# Jaguar predation on domestic horses in the dry forest of northwestern Costa Rica

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## Abstract

Depredation of domestic horses (*Equus caballus*) by jaguars (*Panthera onca*) is an example of human–wildlife conflict that has not received much attention. We monitored spatio-temporal activity and distribution of horses in a 2.64-km<sup>2</sup> fenced area in the dry forest of northwestern Costa Rica in response to 16 jaguar killings of horses during January–November 2017. We monitored 4 horses (2 males, 2 females) equipped with global positioning system transmitters from February–September 2018 to identify daily and seasonal patterns of use of cover types and a water source by horses. We then compared these results to the previous locations where jaguars killed horses to identify the circumstances under which horses seemed more vulnerable to jaguar predation. Based on 1,693 locations, horses spent most time in grassland (92%) rather than forest and edge vegetation (8%) and used a core area of 0.74 km<sup>2</sup> (kernel density estimation) to 0.86 km<sup>2</sup> (minimum convex polygon). Of 16 horse predation events by jaguars, 9 events (56%) occurred in grasslands, 4 in forested areas (25%), and 3 in the forest edge (19%), indicating predation events occurred disproportionately from expected counts based on horse use of vegetation. The predation sites were characterized by a higher proportion of edge and a lower proportion of forest compared to a random points. We suggest that when horses explored areas near the edge of forested areas, the chances of being preyed on by jaguars increased.

**KEYWORDS**

*Equus caballus*, human-wildlife conflict, livestock, management, *Panthera onca*, vegetation use

The killing of domestic livestock by wild carnivores often leads to retaliatory killing and decreases in predator population abundance (Inskip and Zimmermann 2009, Jędrzejewski et al. 2017, van Eeden et al. 2018). Conservation mitigation as result of economic and biodiversity losses is often a priority for all parties concerned (e.g., ranchers, governments, and non-governmental organizations), and thus most efforts have been addressed to better understand the circumstances and environmental factors in which depredation events occur (Wilkinson et al. 2020). In general, poor husbandry and management practices in combination with reduced natural prey often contribute to livestock losses by predators (Inskip and Zimmermann 2009, Ugarte et al. 2019, Rubio-Rocha et al. 2023). Nevertheless, mitigation actions often are site-specific and focus on the location, species, and cultures involved (Zimmermann et al. 2021). Furthermore, there is almost no available research describing the ecological characteristics of livestock as prey animals or the extent to which habitat selection by livestock influences their predation risk (Wilkinson et al. 2020). This information is essential to conduct quantitative assessments of the effects of mitigation interventions that, up to now, rarely have been experimentally tested (van Eeden et al. 2018).

Of the estimated 5.4 billion domestic ungulates censused worldwide in 2022, only about 1% were domestic horses (*Equus caballus*; Food and Agriculture Organization of the United Nations 2023). Nevertheless, the widespread distribution of feral and domestic horse populations makes them an exotic component of ungulate biomass that affects ecological interactions (Boyce and McLoughlin 2021; Morera et al. 2021, 2023). Also, horses are killed by at least 11 large carnivore species (Table S1, available in Supporting Information), though many livestock depredation studies focus on more commonly killed cattle (*Bos taurus*). As a result, the habitat configuration, attributes, and other characteristics of areas with attacks on horses are often ignored or pooled with other livestock in depredation studies (Zimmermann et al. 2005, Michalski et al. 2006, Carvalho et al. 2015, Tortato et al. 2015, Zimmermann et al. 2021).

Jaguars (*Panthera onca*), the largest felids in the Americas, are opportunistic predators that kill cattle, horses, pigs, and goats (Rabinowitz 2005). Combinations of factors such as climate seasonality, forest proximity, vegetation cover, percentage of free-grazing animals, and wildlife occurrence affect the frequency of livestock predation events by jaguars (Zarco-González et al. 2013, Montalvo et al. 2016, Silva-Caballero et al. 2022). Depredation of domestic horses by jaguars is a long-known (Azara 1838, Darwin 1839, Audubon and Bachman 1854, Roosevelt 1914) but little-studied aspect of human-wildlife conflict. Horses are registered as prey in current-day jaguar diet studies (Hayward et al. 2016) and are reported as prey in surveys of livestock depredation (Palmeira et al. 2008, Garrote 2012, Peña-Mondragon and Castillo 2013, Jędrzejewski et al. 2017). Because jaguar predation on horses is relatively low compared to cattle (Sáenz and Carrillo 2002, Amit et al. 2013), conservationists and managers do not have good insights as to the environmental factors influencing this type of predatory event. An understanding of spatial patterns of these predation events can aid in reducing human-jaguar conflicts (Chapman and Reyna-Hurtado 2019, Cruz-González et al. 2021, Silva-Caballero et al. 2022).

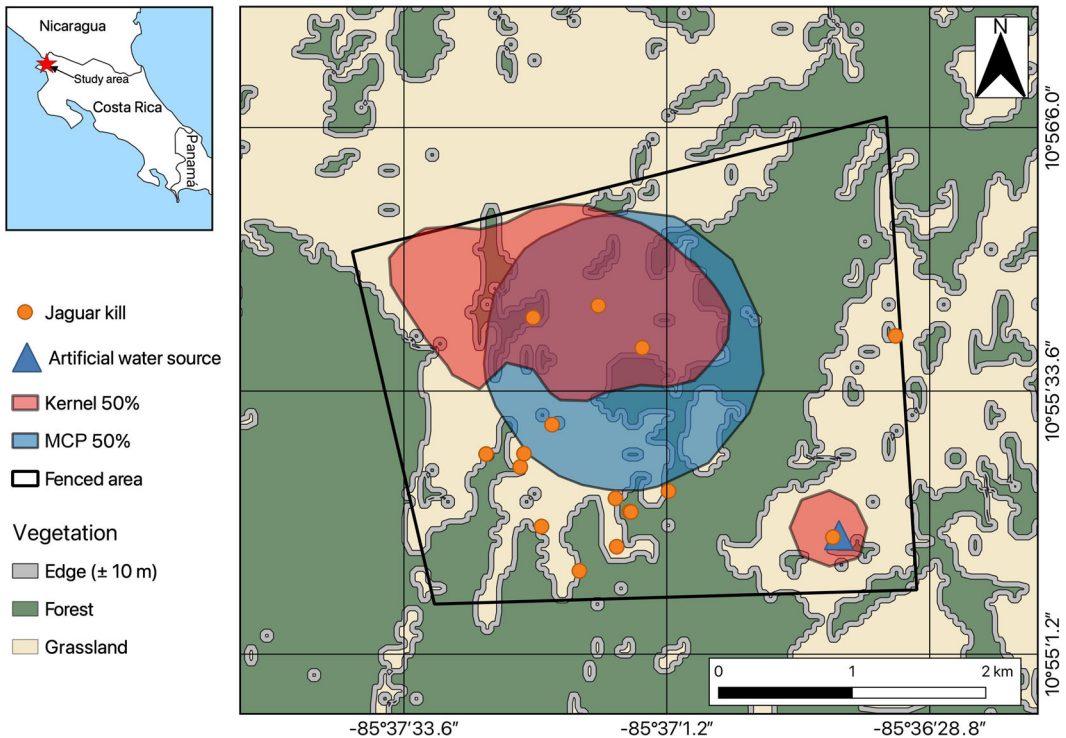
Previously, global positioning system (GPS) satellite units fitted on individual jaguars have been used to identify spatial associations between jaguar kill sites, season, and prey movements (Gese et al. 2016, Silva-Caballero et al. 2022), but few other studies have attempted to monitor relevant prey distribution, mainly because of logistical constraints. Horse movement and habitat use is poorly known (Hennig et al. 2018, Morera et al. 2021), and there is a significant information gap on the spatial ecology of domestic horses in tropical areas and how their distribution correlates to jaguar kill sites.

We initiated this study following the killing of 16 horses by jaguars between January and November 2017 in a fenced horse management area within the dry forest of Santa Rosa National Park in northwestern Costa Rica. At this site we subsequently monitored the movements of 4 horses equipped with GPS tracking units (Feb-Sep 2018)

to assess the distribution and activity of horses within the area. We anticipated that these data would allow us to describe the spatio-temporal patterns between horse movements and jaguar kill sites, and thus suggest horse management options to minimize depredations.

## STUDY AREA

We conducted our study at the Horse Management Site (HMS) in the Santa Elena Sector of Santa Rosa National Park (SRNP), located in the northwestern Costa Rica ( $10^{\circ}55'11.79''\text{N}$   $85^{\circ}36'38.27''\text{W}$ ; Figure 1). The HMS was a fenced area of  $2.64\text{ km}^2$  (elevation = 265–285 m) dedicated to the care and husbandry of horses used by park rangers for operational activities (e.g., surveillance, transport). Periodically, the field staff attended to and performed necessary maintenance. They also diligently monitored the development and growth process of the offspring, including overseeing their weaning. Subsequently, the distribution of the offspring was based on the demand for horses in other sectors. The fencing was made of wooden posts with 3 lines of steel wire, reaching a maximum height of 1.5 m, designed specifically to keep the horses within the fenced enclosure. Other wild animals were able to enter and exit the fenced enclosure without difficulty. At the HMS, the presence of large predators has been documented, including jaguars and pumas (*Puma concolor*), along with mesocarnivores such as ocelots (*Leopardus pardalis*) and coyotes (*Canis latrans*). Additionally, herbivores such as collared peccaries (*Pecari tajacu*) and white-tailed deer (*Odocoileus virginianus*) also have been recorded in the HMS (Morera et al. 2023).



**FIGURE 1** Location of the  $2.64\text{-km}^2$  horse management site (black line) where 4 horses were radio-monitored (Feb–Sep 2018) and distribution of sites where jaguars killed horses (orange dots) in the Santa Elena Sector of Santa Rosa National Park, northwestern Costa Rica. We also present the 50% core area estimates of horse locations with kernel density (red shaded area) and minimum complex polygon (MCP; blue shaded area) methods.

Santa Rosa National Park is one of the few remaining dry forest ecosystems of Central America (Holdridge 2000), and the vegetation is dominated by a mosaic of evergreen and deciduous forest mixed with grass and secondary growth in different regeneration stages (Janzen 2000, Kalacska et al. 2004). During the 1940s, most native dry forest in northwestern Costa Rica was removed owing to the expansion of cattle activity, but in 1971 the Costa Rican government declared the creation of SRNP as an effort to conserve this critical endangered dry forest ecosystem (Janzen and Hallwachs 2016). Though the presence of cattle inside protected areas was not related to the conservation objectives, horses were introduced in SRNP to assist and accelerate the dry forest regeneration process. This action was taken under the hypothesis that horses might act as large fruit tree dispersers, replacing the role of extinct megafauna (Janzen and Martin 1982, Ripple and van Valkenburgh 2010). At the same time, the presence of horses grazing exotic pastures reduced vegetation competition between native species, also diminishing the fuel load (Janzen and Hallwachs 2016). During the last 2 decades, horses inside the SRNP were translocated to the HMS because of management controversies among environmental authorities.

The SRNP has an average annual rainfall of 1,600 mm that is highly seasonal (range = 0–1,040 mm/month); the dry season is December to April (with almost no rain), and the wet season is from May to November (months with  $\geq 40$  mm of rain). The mean annual temperature is 25°C with maximum temperatures of 31°C during the rainy season and  $>35^\circ\text{C}$  during the dry season (Jiménez et al. 2016, Fuller et al. 2020). During the rainy season, free water is abundant at the HMS, as a large part of the area is flooded and drains through small streams. During the dry season, however, the only water available to horses is an artificial water source in the southwestern portion of the area (Figure 1).

## METHODS

During 2017, park rangers managed about 50 horses in the fenced HMS. We recorded 16 horse predation events by jaguars that occurred between January and November, and during early 2018 we revisited sites and noted the geographic coordinates and vegetation type (forest, grassland, or edge; see below) for each predation event. We distinguished whether a jaguar or puma killed a horse by the wound size and location on the carcass, and conditions of the surrounding scene, using a manual for the recognition and evaluation of livestock depredation events by wild carnivores (Márquez and Goldstein 2014). This manual indicates that puma attacks are inconspicuous, lacking visible tears, predominantly targeting the neck or skull of the animal. Subsequently, pumas conceal their prey by covering them with leaf litter, plant material, or soil. On the other hand, jaguar attacks are conspicuous, and show visible evidence of the fracture of the skull or neck vertebrae. During the feeding phase, jaguars exhibit specific selectivity, consuming the throat, lower neck, chest, and areas covering the ribs and scapulae. Unlike pumas, jaguars can drag prey over long distances, sometimes exceeding 1 km, through wooded terrain and slopes. Jaguars generally do not cover their prey with leaves or loose plant material. Thus, during this study all of the predation events analyzed were caused by jaguars (Figure 2).

To better understand spatial factors influencing horse space use in the HMS, we deployed 4 GPS transmitters (Spot Trace©, Globalstar, Covington, LA, USA) on leaders of different horse social groups from February 2018 to September 2018. Each group leader was identified from previous field observations, and by selecting these individuals we hoped to identify the movements of most of the 32 adult horses (23 males, 9 females) that inhabited the HMS during the study. We enclosed the selected horses in a pen located in the HMS and fitted each GPS transmitter on the top of an adjustable horse-collar attached with a plastic tube container on the bottom as an extra battery pack and counterweight (700–1,000 g), like cattle collars used in Botswana (Weise et al. 2019). Each GPS transmitter recorded a location (fix) at 1-hour intervals and registered the date and time. We replaced collar batteries about every 3 weeks. When we concluded the data collection, we removed all GPS transmitters from horses.



**FIGURE 2** Visible evidence of horse predation events by jaguars in horse management site in the Santa Elena Sector of Santa Rosa National Park, northwestern Costa Rica, 2017. View of the areas covering the ribs (A), and the throat, lower neck, chest, scapula (B).

## Data analyses

We estimated the space used and core area for all groups by pooling GPS location data across individuals and applying the 95% and 50% kernel density estimate (KDE) and minimum convex polygon (MCP) methods using the R package *adehabitatHR* (Calenge 2006). We conducted an analysis to assess the frequency of GPS-tracked horse locations in dry and wet seasons, considering the time of day as a distinguishing factor (daytime [0501–1800] or nighttime [1801–0500]). Using this dataset, we investigated patterns in the horses' preference for different vegetation types. To examine variations in vegetation type use across seasons and times of the day, we employed chi-square tests for our analysis. Additionally, we conducted a water distance analysis using a generalized linear mixed model implemented with the *lme4* R package (Bates et al. 2015). The response variable was the distance to the artificial water source for each GPS location of the horses. The fixed factors considered were the season (dry or wet) and the time of the day (day [0501–1800] or night [1801–0500]), and we included the individual ID as a random factor. To assess the statistical significance of the fixed factors, we performed a likelihood ratio test using the *lmtest* R package (Zeileis and Hothorn 2002).

This study aimed to analyze predation events within the HMS by characterizing their spatial distribution and vegetation characteristics. To achieve this, we first compared the characteristics of the 16 predation sites with those of 16 randomly selected sites. To characterize the vegetation, we designated the strip generated by a 10-m buffer along the border between pasture and forest as the edge. Additionally, because predation may be influenced by the immediate, fine-scale characteristics of a landscape (Davie et al. 2014), we arbitrarily created a 100-m buffer around each point (both observed and random) to calculate the proportion of edge, forest, and grassland cover. We

used the nearest neighbor analysis tool of QGIS.3.16 (QGIS Development Team 2021) to test whether the patterns of point distribution differed from a simulated random distribution pattern; thus, we contrasted the observed and expected mean distance with a 1-tailed *P*-value using the *pnorm* function in the R base package (R Core Team 2021). We compared the frequency of predation events in grassland, forest, and edge vegetation areas, and inside or outside of the horse core use area, with chi-square tests. We compared the mean proportion of each cover type between random and observed points using 100 randomizations and *t*-tests. We also compared the mean distance to the edge and water source of the predation and random points using a *t*-test.

We then compared the observed counts of predation by vegetation type (forest, edge, grassland) with the expected counts based on the vegetation use of horses, using a chi-square test. Additionally, we compared the mean distance of predation events and GPS locations of horses to the water source using the non-parametric Wilcoxon test. We carried out the analyses with the statistical software R (R Core Team 2021).

## RESULTS

On average, each horse was tracked for 41 days (range = 9–105 days), yielding 1,693 locations (Table 1). Horse space use estimates, derived from the 95% MCP and 95% KDE methods, revealed space use areas of 2.45 km<sup>2</sup> and 2.91 km<sup>2</sup>, respectively, recognizing that the fenced area measured 2.64 km<sup>2</sup> and emphasizing that horse movement and space used would be limited to the enclosed space. The 50% horse core areas for MCP and KDE methods were 0.86 km<sup>2</sup> and 0.74 km<sup>2</sup>, respectively. The kernel density method also identified a small core area in the southeast of the study area associated with the presence of an artificial water source (Figure 1).

Horses used a higher proportion of grasslands (Table 2). During the daytime (vs. nighttime) horses used more forest and edges ( $\chi^2 = 24.65$ ,  $P = 0.01$ ). The frequency of vegetation use during the wet season indicated a decreasing pattern in the use of forest and edges compared with the dry season (Table 3), and during nighttime in the wet season horses avoided the forest and the edges, showing no statistical evidence of a difference from daytime locations ( $\chi^2 = 4.59$ ,  $P = 0.13$ ). The water distance analysis revealed variations in space use of horses based on the season and time of day (likelihood ratio test;  $\chi^2 = 23.27$ ,  $P < 0.01$ ). Specifically, when comparing seasons, the distance to the artificial water trough was 0.24 and 0.22 times shorter during the dry season compared to the wet season in the daytime and nighttime, respectively ( $P < 0.01$ ). Similarly, it was 0.11 times shorter during the dry season during the day than the dry season at night ( $P < 0.01$ ). Furthermore, during nighttime, the distance in the dry season was 0.13 times shorter than in the wet season ( $P = 0.03$ ). We did not observe differences between the wet season in the daytime and the dry season at night or between the wet season in the daytime and the wet season at night ( $P > 0.05$ ).

We recorded 16 events of horse predation by jaguars. The observed distance between predation locations (207 m) was higher than the expected distance (155 m, based on random points), hence the data indicated no clustering in distribution ( $Z = 2.55$ ,  $P = 0.99$ ). Nine events (56%) occurred in grasslands, 4 in forested areas (25%), and 3 in the forest edge (19%), not differing from a random point distribution ( $\chi^2 = 0.66$ ,  $P = 0.72$ ). On average,

**TABLE 1** Monitoring effort of 4 horses radio-tracked with global positioning system collars in the horse management site of the Santa Elena Sector of Santa Rosa National Park, northwestern Costa Rica, February to September 2018.

Horse ID	Dates	Number of days monitored	Number of locations	Number of locations/day
3 (female)	3 Feb–12 Feb 2018	9	185	20.6
1 (male)	7 Feb–23 May 2018	105	808	7.7
4 (female)	8 Feb–25 Feb 2018	17	354	20.8
2 (male)	29 Aug–30 Sep 2018	32	346	10.8

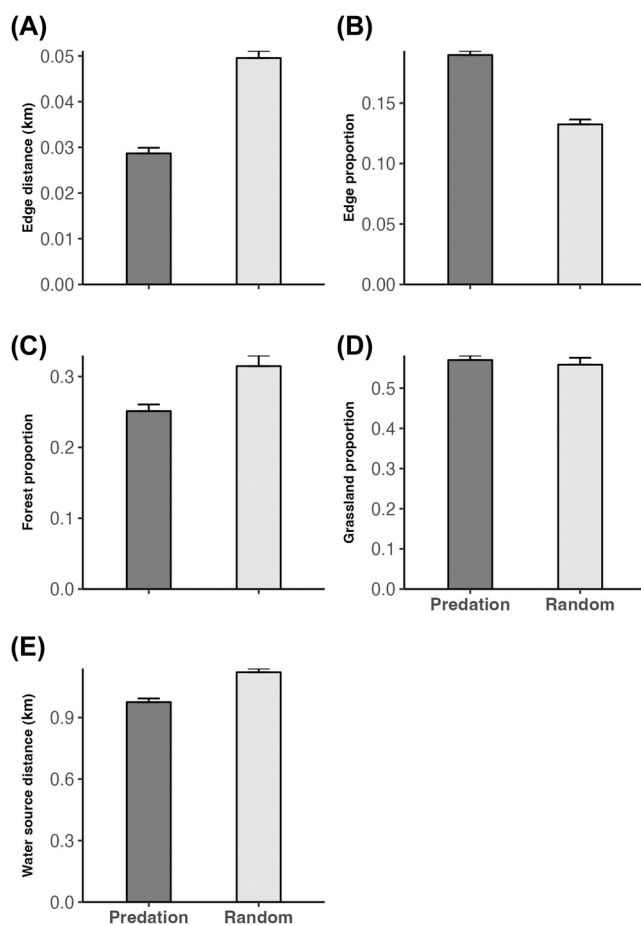
**TABLE 2** Monitoring effort, percent of locations in vegetation types, and distance ( $\pm$ SE) to artificial water source during daytime (0501–1800) and nighttime (1801–0500) intervals of 3 horses radio-tracked with global positioning system collars during the dry season (Jan–Apr and Dec 2018) in the horse management site of Santa Elena Sector of Santa Rosa National Park, northwestern Costa Rica.

Time of day	Individual	Number of days monitored	Number of locations	Percent of locations			Mean distance to artificial water source (km)
				Forest	Grassland	Edge	
Daytime	1 (male)	82	318	7.2	79.2	13.5	1.11 ( $\pm$ 0.03)
	3 (female)	9	99	3.0	80.8	16.2	1.04 ( $\pm$ 0.05)
	4 (female)	17	201	13.4	70.7	15.9	0.85 ( $\pm$ 0.03)
	Mean	36	206	7.9	76.9	15.3	1.01 ( $\pm$ 0.02)
	Total	108	618	8.6	76.7	14.7	
Nighttime	1 (male)	82	280	5.0	88.2	6.8	1.16 ( $\pm$ 0.03)
	3 (female)	9	86	0.0	94.2	5.8	1.28 ( $\pm$ 0.04)
	4 (female)	17	153	4.6	84.3	11.1	0.99 ( $\pm$ 0.03)
	Mean	36	173	3.2	88.9	7.9	1.13 ( $\pm$ 0.02)
	Total	108	519	4.1	88.1	7.9	

**TABLE 3** Monitoring effort, percent of locations in vegetation types, and distance ( $\pm$ SE) to artificial water source during daytime (0501–1800) and nighttime (1801–0500) intervals of 2 horses radio-tracked with global positioning system units during the wet season (May–Nov 2018) in the horse management site of Santa Elena Sector of Santa Rosa National Park, northwestern Costa Rica.

Time of day	Individual	Number of days monitored	Number of locations	Percent of locations			Mean distance to artificial water source (km)
				Forest	Grassland	Edge	
Daytime	1 (male)	23	117	6.8	82.9	10.3	1.26 ( $\pm$ 0.05)
	2 (male)	32	168	1.8	91.1	7.1	1.27 ( $\pm$ 0.02)
	Mean	27.5	142.5	4.3	87.0	8.7	1.26 ( $\pm$ 0.02)
	Total	55	285	3.9	87.7	8.4	
Nighttime	1 (male)	23	93	2.2	92.5	5.4	1.37 ( $\pm$ 0.05)
	2 (male)	32	178	0.6	91.0	8.4	1.24 ( $\pm$ 0.02)
	Mean	27.5	135.5	1.4	91.7	6.9	1.28 ( $\pm$ 0.02)
	Total	55	271	1.1	91.5	7.4	

predation events were a mean distance of 29 m to the forest edge, differing from a random point distribution (mean distance = 47 m;  $t_{186.95} = 20.78$ ,  $P < 0.01$ ). Predation sites (within 100-m radius) were in different vegetation assemblages: 19% on the edge of forest vegetation, 25% in forest, and 56% in grassland. Predation sites had a higher proportion of edge ( $t_{192.48} = 21.40$ ,  $P < 0.01$ ), and a lower proportion of forest ( $t_{166.01} = 3.13$ ,  $P < 0.01$ )



**FIGURE 3** Average comparisons of edge distance (A), proportions of edge (B), forest (C), and grassland (D; within a 100-m radius), and distance to water sources (E) between jaguar predation sites (dark gray bars) and random locations (light gray bars) inside the horse management site in the Santa Elena Sector of Santa Rosa National Park, northwestern Costa Rica, 2017–2018. Error bars represent 95% confidence intervals.

compared with a random point distribution (Figure 3), while the proportion of grassland did not show statistical evidence of differences between the observed pattern and the one generated randomly ( $t_{170,24} = 1.12$ ,  $P = 0.26$ ; Figure 3). On average, predation sites were located closer to the artificial water source compared to randomly distributed points ( $t_{197,99} = 11.3$ ,  $P < 0.01$ ; Figure 3).

Jaguar predation events on horses differed from expected counts based on horse use of vegetation ( $\chi^2 = 14.65$ ,  $P < 0.01$ ). In grasslands, predation was 0.66 times lower than expected, while in forests and edges, it was 4.8 and 1.8 times higher than expected, respectively. Furthermore, predation occurred 0.85 times closer to water than the mean distance of the horse's GPS location to water ( $W = 17348$ ,  $P = 0.05$ ).

## DISCUSSION

Our findings about jaguar predation on horses in the dry forest were consistent with previous evidence of jaguar preying on other livestock species within its range (Cavalcanti and Gese 2010, Gese et al. 2016, Montalvo et al. 2016) and with other predators such pumas (Turner et al. 1992, Andreasen et al. 2021). Horse movement in

this fenced study area necessarily indicated small space use areas (50% horse core areas = 0.7–0.9 km<sup>2</sup> within the 2.64-km<sup>2</sup> HMS area), which is much lower compared to a free-ranging wild population (e.g., ~117 km<sup>2</sup>; Andreasen et al. 2021).

By integrating data from GPS-collared horses and horse predation events by jaguars, we observed that horses in SRNP use the habitat similarly to horses in North America (Hennig et al. 2018) in that they preferred pastures over forest vegetation, and rarely used dense forest vegetation unless perhaps as movement corridors between pastures (Hansen et al. 2009, Massé and Côté 2012), making horses more vulnerable to jaguar attacks. Ganskopp and Vavra (1986) reported similar results in the Oregon's Owyhee Breaks, where horses primarily used pastures, and inter-pasture movement of horses throughout natural forested boundaries to access other resources such as water sources and natural salt reservoirs. The GPS technique reveals that our findings are consistent with other studies assessing water resource use in equids, demonstrating higher usage of this resource during hotter hours or seasons. Consequently, management plans could prioritize mitigation programs targeting these areas (Hennig et al. 2023, Karish et al. 2023).

Jaguar kill sites were associated with forest, edges, and water proximity as a pattern previously observed in site predation records. Therefore, we hypothesized the high frequency of horse predation events near (<29 m) from forested areas is likely related to the ambush and opportunistic behavior of the jaguar described by others (Rosas-Rosas et al. 2010, Gese et al. 2016).

The occurrence of horse predation events does not show a robust predator-prey relationship typical of other events with wild prey (De Oliveira 2002, Carrillo et al. 2009). This suggests that jaguar predation of horses is rare compared to predation of natural prey (Cruz-González et al. 2021, Flores-Martínez et al. 2022), and the occurrence of predation on horses can be attributed to the unique characteristics of the study site, coupled with the opportunistic nature of jaguars. Thus, we expect that common prey available inside SRNP, especially peccaries and white-tailed deer (Montalvo et al. 2019), would sustain a healthy jaguar population (Montalvo et al. 2015, 2022). Though our datasets were not collected at the same temporal scale, all data were collected in the same study area; still, our results should be carefully interpreted to avoid misleading conclusions, as our sample sizes were small.

## MANAGEMENT IMPLICATIONS

Our study suggests that horse predation by jaguars, though rare, is still likely to occur in places with healthy and abundant natural prey species, which reduces jaguar dependence on horses. In addition, the low frequency of historical predatory events suggests that jaguars may be carefully selecting their prey to maximize their success in the hunt. Livestock predation should be related to aspects of herd management. Based on this study, we recommend keeping the horses, particularly those in fenced areas, within core grassland areas away from the forest edges to reduce killings. Though forest cover cannot be removed in the park, removal of significant cover in other pasture areas seems a reasonable management consideration. Moreover, long-term monitoring of jaguar and natural prey densities will contribute to a better understanding of the seasonal patterns of horse depredation by jaguars and how this predator responds to variations in the availability of natural prey within and near the HMS.

## ACKNOWLEDGMENTS

We thank R. Blanco and the personnel of Área de Conservación Guanacaste for their cooperation and assistance in the field and Idea Wild, Café Britt, and the University of Massachusetts Amherst for providing equipment.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## ETHICS STATEMENT

We followed the ethics and guidelines of the American Society of Mammalogists (Silkes et al. 2011) with the approval of the Environment Minister of Costa Rica (ACG-PI-034-2017).

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*Associate Editor: Francesco Ferretti.*

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**How to cite this article:** Morera, B., V. Montalvo, J. Moya, J. Obando, C. Sáenz-Bolaños, T. K. Fuller, and E. Carrillo. 2024. Jaguar predation on domestic horses in the dry forest of northwestern Costa Rica. *Journal of Wildlife Management* e22637. <https://doi.org/10.1002/jwmg.22637>