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**DRIVERS OF JAGUAR (*PANTHERA ONCA*) DISTRIBUTION, DENSITY, AND MOVEMENT  
IN THE BRAZILIAN PANTANAL**

by

Allison Loretta Devlin

A thesis  
submitted in partial fulfillment  
of the requirements for the  
Doctor of Philosophy Degree  
State University of New York  
College of Environmental Science and Forestry  
Syracuse, New York  
June 2019

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## Acknowledgements

I am indebted to many mentors, colleagues, friends, and loved ones whose guidance, support, patience, and constructive challenges have carried this project to its culmination. Not only have each of you contributed to this research, you have also been instrumental in developing my scientific acumen and personal character in such a way that I find it difficult to fully express my gratitude. For the dizzying elation, crushing pressure, and light at the end of this long, winding tunnel, I thank each and every one of you for the lessons you have taught me and the values you have instilled in me.

Thank you first and foremost to Dr. Jacqueline L. Frair, in title my major advisor but in reality so much more. Through the years, your scientific rigor and unwavering commitment to the pursuit of truth have shaped my understanding of what it exactly means to be a scientist. Where life may take unexpected twists and challenges may arise, you have taught me to keep the goal of pursuing truth clear in mind and to be uncompromising in quality and scientific rigor. I am forever grateful to your mentorship and look forward to carrying these lessons with me throughout my career and my life.

To my academic committee, thank you for your support over the years. Dr. James Gibbs, you have taught me to navigate the nuances of balancing academia with on-the-ground field research, and of the importance of maintaining scientific and diplomatic leadership in this era of urgency. Dr. Jonathan Cohen, thank you for making challenging courses enjoyable and always being approachable with statistical inquiries. And to my committee chair, Dr. Stephen Stehman, thank you for bringing your enthusiasm and curiosity to help lighten the most stressful parts of this dissertation process.

To my committee members and mentors in the big cat world, I am forever grateful. To those who served on my committee – Dr. Luke Hunter and Dr. Peter Crawshaw Jr. – thank you for your patience and guidance throughout this project, and throughout my career. Your expertise has helped to shape this dissertation to be not only academically relevant, but to also keep it (and me) grounded in ecology and conservation focused on the needs of wild felids. To field team members and mentors past and present at Panthera, Dr. Howard Quigley, Dr. Alan Rabinowitz, Dr. Rafael Hoogesteijn, Dr. Fernando Tortato, Dr. Bart Harmsen, Dr. Rebecca Foster...and so many more, I cannot imagine being in this field without each of you and am grateful to know that each and every one of you is on the side of the world's wild cats.

I thank my friends and colleagues at SUNY College of Environmental Science and Forestry (Syracuse, NY, USA), Panthera Foundation (New York, NY, USA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio; Parque Nacional do Pantanal-Matogrossense, Mato Grosso, Brazil), and CENAP \ ICMBio (Atibaia, SP, Brazil), Fundação Ecotrópica (Cuiabá, MT, Brazil), and Instituto Homem Pantaneiro (IHP; Corumbá, Mato Grosso do Sul, Brazil) for logistic, financial, and analytical support. In Brazil and in the Pantanal, I extend my deepest gratitude to Elizeu Evangelista da Silva, Grandão, Suelen Leite, Thiago Semedo, Nuno Rodrigues da Silva, Zilma Pereira Silva de Oliveira, José Augusto Ferraz de Lima, Florêncio, Clarindo, the Eberhards, Paulo Rogerio Silva, André de Botton, Elza and Hildebrando Costa, and Vicente. I am indebted to the Pantaneiro cowboys and families at Fazendas São Bento and Jofre Velho for invaluable assistance throughout this field study.

This dissertation is dedicated to my family, Kevin, Susan, Brittany, and Eric Devlin. Thank you for your patience and support, and for keeping me laughing throughout this project.

Ethical statement: My research was supported by Panthera's Kaplan Graduate Award Program, with logistic and in-kind support from ICMBio, Fundação Ecotrópica, and IHP. All activities were permitted by the Brazilian government (CNPq n° 000179/2010-8; SISBIO n° 21447-4; SISBIO n° 18699-2) and SUNY-ESF Institute of Animal Care and Use Committee (IACUC, valid 31 March 2011 - 31 May 2014). I studied in Brazil under Research Visa VITEM I (n° 050777MH).

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## ABSTRACT

A.L. Devlin. Drivers of jaguar (*Panthera onca*) distribution, density, and movement in the Brazilian Pantanal, 211 pages, 14 tables, 9 figures, 2019. *Ecology* journal style guide used.

Globally, conversion of land for livestock production is a major driver of changes in prey availability for and conflict with large carnivores – notably so for Neotropical species including jaguars (*Panthera onca*). Using camera traps and GPS-collared individuals, I investigated the degree to which jaguars altered their activity patterns, population density, and selection of resources in response to native and non-native prey, and the degree to which these processes interacted (e.g., density-dependent resource selection), across a network of protected areas and working cattle ranches (where hunting of jaguars was prohibited) in the Brazilian Pantanal. Overall, I found that local jaguar populations were more patchily distributed in the ranches and more uniform in the parks, with the most consistent driver of distribution being canopy cover. Similar trends were observed for the activity and distribution of wild prey in the parks, although within the ranches cattle (*Bos taurus*) and feral water buffalo (*Bubalus bubalis*) were important drivers. Both temporal and spatial jaguar activity positively and most consistently tracked with wild prey, and negatively with cattle. Canopy cover and a composite of wild prey activity drove local jaguar density in both the parks and ranches. In the ranches, jaguar densities tended to be higher within remaining forest patches – such that, on average, jaguar density was statistically similar between the ranches and the parks. Jaguar density, wild prey and cattle availability, and forest canopy cover influenced local resource selection by jaguars. From broad (home range) to fine (foraging steps) scales, forest cover was the single-most consistent metric predicting prey and jaguar distributions – underscoring the importance of forest cover for wildlife conservation in the Neotropics, spotlighting concerns over recent and pending changes land use policy throughout jaguar range, and indicating a potentially simple metric for monitoring jaguar habitat potential where they are protected from hunting. Importantly, despite increasingly rare and fragmented forest cover in ranching landscapes, the “wildlife-friendly” practices in my study area helped to support a density of jaguars equivalent to protected areas with intact forest canopies, indicating their potential value as a conservation tool.

Key Words: activity pattern, Brazil, conservation, density, ecology, human-wildlife conflict, jaguar *Panthera onca*, livestock, Pantanal, prey, relative activity index, resource selection function, spatially-explicit capture-recapture, step selection function, wetland, wildlife

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## CHAPTER 1: INTRODUCTION

### THE FRONTLINES OF CARNIVORE CONSERVATION: PROTECTED AREA EDGES

Managing the persistence of wildlife populations in disturbed landscapes remains a fundamental challenge in ecology (Mitchell and Hebblewhite 2012). Given that the existing base of terrestrial protected areas around the world is insufficient to sustain many large mammalian species (Mitchell and Hebblewhite 2012), conservation efforts in recent decades have shifted to establishing and maintaining connectivity between core population units (i.e., sources) that protected areas presumably support. Multiple-use landscapes immediately adjacent to protected areas are often managed in support of human population needs. Such multi-use landscapes are critical for population connectivity but often function as population sinks (Woodroffe and Ginsberg 1998) – especially as they often absorb dispersers yet do not facilitate successful passage of those individuals to other source populations. Wildlife corridors must provide conditions sufficient for wildlife to persist and maintain potential productivity. But how can functional connectivity be successfully established and maintained?

With human population growth rates accelerating along protected area boundaries (Wittemyer et al. 2008), effective conservation interventions must balance the needs of both wildlife and human populations (Armenteras et al. 2017). In cases of human-wildlife conflict involving large predators, perceived or actual risks to safety (Beckmann and Berger 2003, DeStefano and Deblinger 2005) and loss of livestock (Treves and Karanth 2003, Cavalcanti and Gese 2010, Marchini and Macdonald 2012) drive high predator mortality rates. Increased tolerance for risk is required among the human populations that share the landscape with predators, especially if multi-use landscapes are to function as effective corridors. Therefore, novel conservation solutions are needed.

One such attempt to facilitate connectivity and human tolerance is currently underway for jaguars (*Panthera onca*), where eco-tourism focused on jaguar viewing is being developed to offset cattle (*Bos taurus*) losses and spur local economies in favor of jaguar persistence (Tortato et al. 2017a). The research herein seeks insights into how jaguars use working landscapes when mortality pressure has been



effectively removed. In particular, I studied the activity, density, and resource selection of jaguars and their medium- to large-bodied prey within a “wildlife-friendly” ranching complex and a nearby complex of fully protected areas. In particular, I explored the degree of demographic similarity in jaguar populations between the two regions, anticipating that transient male jaguars may dominate the disturbed ranchlands, leading to higher levels of infanticide, suppressed productivity, and lower potential viability for population persistence. Moreover, anticipating that jaguars would be concentrated in smaller remnant forest patches within the ranchlands, I evaluated the degree to which local movement and resource selection decisions might change with local conspecific density – thus, assessing the degree to which past studies of jaguar resource selection and dispersion (primarily derived from protected areas) might be relevant to human-modified landscapes. Lastly, I evaluated the degree to which jaguars might switch their focus, in terms of activity periods, dispersion, and resource selection, to domestic cattle over wild prey, which could have severe implications for both cattle producers and jaguar conservation.

#### FOCAL STUDY SPECIES AND STUDY AREA

The jaguar is currently listed as Near Threatened by the IUCN (Quigley et al. 2017), and found throughout the Neotropics in a mosaic of habitat with varying land use patterns (Azevedo and Murray 2007, Rabinowitz and Zeller 2010). This predator is the third largest felid in the world and the largest in the western hemisphere (Quigley et al. 2017). Jaguars exhibit a solitary social structure except when mating or when females rear their young (average litter size of 1-4 cubs) until the offspring reach age of dispersal (e.g., 1.5-2 years old; Quigley et al. 2017). Jaguars opportunistically consume over 80 different prey species (Foster et al. 2010), including foremost: white-lipped peccary (*Tayassu pecari*); collared peccary (*Pecari tajacu*); red and grey brocket deer (*Mazama americana*; *Mazama gouazoubira*, respectively); and more aquatic species like caiman (*Yacare caiman*) and semi-aquatic capybara (*Hydrochoerus hydrochaeris*). While jaguars primarily occur in closed habitat with smaller prey, as

evidenced by adaptive and behavioral plasticity, these apex predators persist in a variety of habitat with small- to large-bodied prey species, from agouti (*Dasyprocta* spp.) to tapir (*Tapirus terrestris*).

Clearing of intact habitat, especially for monoculture or grazing pastures for ranching activities, drives most deforestation in Latin America (Armenteras et al. 2017). Major direct drivers of deforestation include agriculture (20.5%), cattle grazing (13.4%), and expansion of infrastructure including roads (12.5%; Armenteras et al. 2017). Conversion of forests to pasture for cattle ranching is common throughout the Neotropics, with the majority of deforestation occurring in South America (Aide et al. 2013). For jaguars, one of the remaining population strongholds is in the Brazilian Pantanal (Quigley and Crawshaw 1992, Sanderson et al. 2002, Rabinowitz and Zeller 2010). Over 85% of the Pantanal is dedicated to large-scale ranching (Alho et al. 1988) and about 5% is federally protected (Alho and Sabino 2011, Tomas et al. 2019). In cattle ranches, the augmentation (increased availability) of food resources (e.g., cattle carcasses) has multiple potential impacts – including, for example, exacerbating intraspecific conflict by bringing together individual predators like jaguars that would normally avoid each other – potentially increasing levels of intraspecific strife such as infanticide (Tortato et al. 2017b). This dissertation was conducted in two distinct sites in the northern Brazilian Pantanal: a protected area and a “wildlife-friendly” (i.e., in addition to following all legislation, does not persecute, hunt, or retaliate against any wildlife species; engages in conflict mitigation techniques; Quigley et al. 2015) working cattle ranch complex. This design offered unique opportunities to test hypotheses on species activity, distribution, and behavior in areas with different management techniques.

## STUDY OBJECTIVES

This dissertation involves a multi-part, integrated analytical framework to address questions on the drivers of jaguar distribution and movement in protected and working landscapes (Fig. 1-1). The dissertation is structured such that each data chapter (Chapters 2, 3, and 4) is prepared as an individual

manuscript, and follows formatting guidelines for text, table, figure, and references in preparation for submission to appropriate ecology- and conservation-focused peer-reviewed journals (e.g., *Ecology*).

To understand the spatio-temporal availability of prey resources, and determine what drives predator activity within working landscapes, in Chapter 2 I first investigated the comparative activity of predators, native herbivores, and domestic ungulates in the parks and the cattle ranches. I used camera trap records to develop activity pattern overlap for each study site per survey-year. The herbivore species were first evaluated singly, then in composite, to understand what characteristics (e.g., species-specific activity and availability; aggregate activity of available protein) drive predator activity in each study area. I hypothesized that generalist predators like jaguars would respond to species-specific and overall availability of prey (composite relative activity of prey), to maximize hunting efficiency and balance that with intraspecific strife anticipated by the high degree of overlap in activity of jaguars.

In Chapter 3, I explored jaguar density as a function of security cover and prey (wild and domestic) availability using spatial capture-recapture approaches based on camera trap surveys. I expected female jaguar densities to increase with increasing food resources, whereas densities of territorial males were expected to be a saturating function of female density (Andren 1990, Goodrich et al. 2010). I expected to observe deviations from this pattern in working landscapes, especially given the provision of large-bodied food resources (cattle) expected to support high local densities and, by extension, elevated levels of intra-specific strife.

In Chapter 4, I sought insight into how and why individual jaguar movement and resource use is influenced by dynamic resource availability and conspecific densities. More specifically, I addressed the question: if jaguar densities are patchier in working landscapes, might local density and dynamic availability of resources be important predictors of animal movement decisions? Resource selection analyses provide only a static snapshot in time and in population conditions. There is an explicit need to include density dependence and stochastic representations of resource availability (e.g., spatio-temporal availability of prey) to provide a more dynamic and informative understanding of selection (McLoughlin

et al. 2010). Currently, patterns of resource selection have been integrated into spatial capture-recapture models to better predict local animal density (Efford 2016), but herein I flip that approach on its head and instead investigate how local conspecific density and prey availability informs the resource selection process (Potts et al. 2014, Avgar et al. 2016, Signer et al. 2019) for telemetered jaguars.

Finally, in Chapter 5 I provided a synthesis on the broader implications of each data chapter. Specifically, I interpreted the conclusions drawn from each data chapter based on past, current, and future directions in carnivore management. In the dynamic and multi-use landscape of the Brazilian Pantanal, management is rapidly expanding for livestock production while, in some sites, the local economy is changing due to a growing ecotourism industry. Securing the future of jaguars and other carnivores within and outside protected areas is complex and will require adaptive management in rapidly changing conditions. Each data chapter examines questions and draws conclusions from the underpinning mechanisms which drive jaguar activity, density, and movement. Such insights provide a foundation upon which recommendations can better guide conservation action and management decision-making to support the persistence of carnivores like jaguars within multi-use and rapidly changing landscapes.

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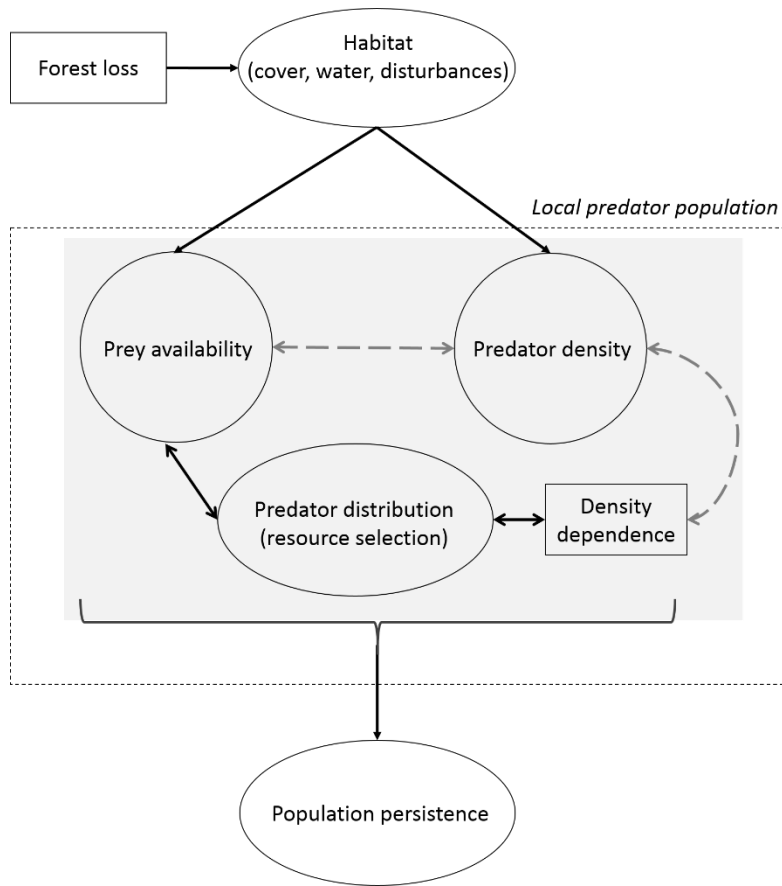


Figure 1-1. Conceptual model of interactions between resources and predator population dynamics.

Interactions are mediated by factors including forest loss (e.g., conversion to pasture for cattle ranching) and density-dependent processes (solid boxes), which ultimately inform population persistence of the local predator population (dashed box). This dissertation focuses on the shaded area to quantify prey availability, predator density, and density-dependent resource selection in a population of jaguars in the northern Brazilian Pantanal.



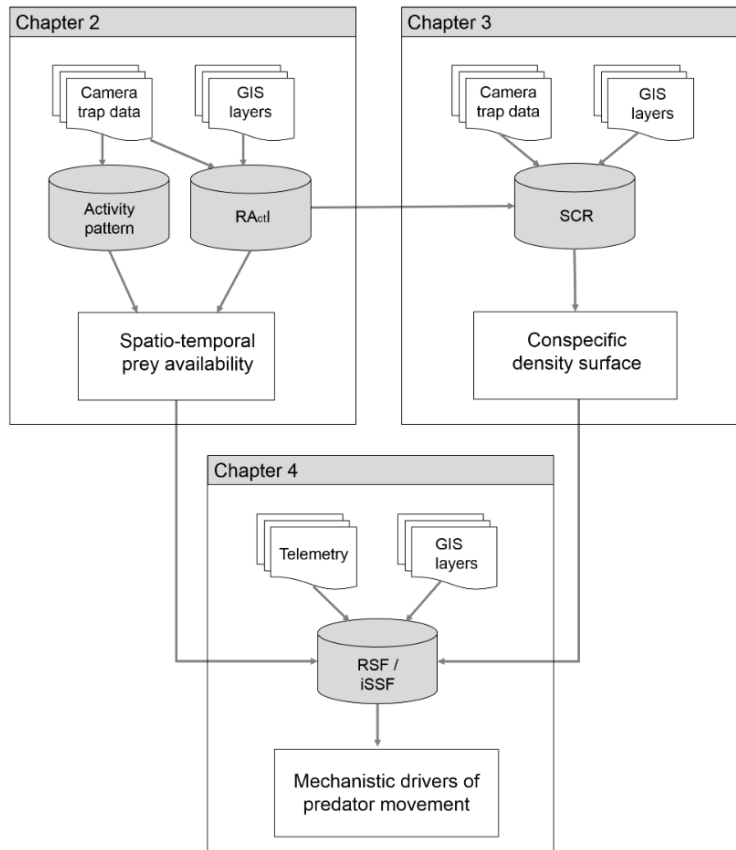


Figure 1-2. Dissertation workflow demonstrating the integration of resource availability, population densities, and resource selection and movement of jaguars in the northern Brazilian Pantanal. In Chapter 2, I developed spatio-temporal prey activity surfaces derived from camera trap data and GIS layers to inform activity pattern and relative activity index ( $RA_{ctI}$ ) analyses. In Chapter 3, I evaluated the drivers of jaguar density by using spatially-explicit capture-recapture (SCR) and included covariates for prey availability (predicted prey activity surfaces,  $RA_{ctI}$ ; Chapter 2) and landscape covariates including security cover (derived from GIS layers). Finally, in Chapter 4, I investigated the mechanistic drivers of jaguar movement using GPS data collected from telemetered individual jaguars to inform resource selection and integrated step selection functions (RSF; iSSF), to quantify the behavioral response of individuals to security cover, dynamic availability of food resources (Chapter 2), and conspecific density (Chapter 3).

**CHAPTER 2: MOTIVATING THE HUNT: OVERLAPPING ACTIVITY AND DISTRIBUTION  
OF JAGUARS (*PANTHERA ONCA*) AND THEIR PREY  
IN A NEOTROPICAL WETLAND**

**ABSTRACT**

For native wildlife, working landscapes introduce elevated levels of disturbance including habitat loss and fragmentation, novel competitors or prey, and mortality risks. Greater understanding of the interactions among wild herbivores and livestock, and the knock-on effects to large predators, is needed to effectively maintain diverse and thriving ecosystems under ever-increasing human demands for livestock production. The objectives of this study were to (1) evaluate the temporal activity pattern overlap ( $\hat{\Delta}$ ) and (2) spatial distribution in activity of native herbivores, jaguars (*Panthera onca*), and domestic ungulates in the Brazilian Pantanal. I compared the spatio-temporal activity patterns of small- to large-bodied native wild herbivores, domestic livestock including cattle (*Bos taurus*), and jaguars within disturbed forest systems (i.e., working ranches where hunting was excluded) and nearby intact forest systems (i.e., protected areas where livestock, agriculture, and hunting were excluded). Using camera trap data collected over 3 consecutive years, I observed temporal patterns of activity to be similar within species across study areas. In the ranches, the jaguar activity overlapped with cattle ( $\hat{\Delta} = 0.44$ , 95% CI = 0.38-0.50) significantly less than wild prey ( $\hat{\Delta} = 0.88$ , 95% CI = 0.85-0.92), while in both study areas jaguars had the greatest overlap in activity with brocket deer (*Mazama* spp.;  $\hat{\Delta} = 0.93$ , 95% CI = 0.88-0.96). Wild herbivore activity generally increased with percent forest cover and decreased in areas of higher cattle activity. The spatial distribution of jaguar activity in the ranches increased with forest cover and a composite of wild herbivore activity in the ranches, and in the parks positively tracked with cover and brocket deer activity. Although forest canopy was reduced and patchier in the ranches compared to the parks, the spatial distribution of animal activity was patchier in the parks likely due to stochastic environmental conditions including seasonal flooding. The results indicate that there were slight shifts in activity peaks and distribution of

wildlife activity were mainly driven by canopy cover. Wildlife species may subtly shift or restrict activity periods, and concentrate their distribution among intact patches of habitat; by doing so, this may substantially increase survival probability or reduce competitive costs, thereby enabling native species to successfully exploit human-modified environments.

KEY WORDS: activity pattern; carnivore; herbivore; livestock; *Panthera onca*; protected area; ranch; relative activity index

## INTRODUCTION

For predators, perhaps no landscape is more enticing yet more risky than areas supporting livestock production. Worldwide, 26% of terrestrial land is devoted to livestock production (Steinfeld et al. 2006, Thornton 2010). Livestock are typically managed in more productive landscapes, especially in comparison to protected areas. Protected areas are typically set aside in areas which are unproductive, aesthetically beautiful, or otherwise unsuitable for human use. Thus, wildlife – including predators – are likely drawn to productive landscapes. Due to the increasing rate of expansion in development of natural areas for human use, including clearing of intact forest to create pasture for livestock ranching (Noss 1994, Steinfeld et al. 2006), this brings otherwise elusive predators into consistent conflict with livestock managers, either due to perceived or actual threat to livestock and / or human safety (Treves and Karanth 2003, Herrero et al. 2009). Across the globe, an estimated 2.6% of livestock are annually lost to predators (Graham et al. 2005) and over 75% of all felid species are impacted by some form of human-wildlife conflict (Inskip and Zimmermann 2009). Conservation and management programs aim to mitigate such conflict and threats. Such threats may be mitigated by the adoption of “wildlife-friendly” management of ranching operations, which includes applying effective anti-predation techniques to reduce risk of predation on livestock by predators, supporting populations of wild prey species through maintaining intact habitat and no hunting pressure, and no persecution of the predator itself (Quigley et al. 2015).

For native wildlife, working landscapes involve habitat loss and fragmentation, novel competitors or prey, elevated levels of disturbance, and novel or elevated mortality risks (Treves and Karanth 2003, Graham et al. 2005). Evolutionary constraints may limit species adaptability to highly modified environments, as evidenced by intra-specific synchrony in peak activity patterns throughout their range (Aschoff 1966, Kronfeld-Schor and Dayan 2003). For example, species of Rodentia and Neotropical deer (*Mazama* spp.) demonstrate range-wide phylogenetic synchrony in timing of daily activity peaks (Rivero et al. 2005, Roll et al. 2006, Kronfeld-Schor and Dayan 2008, Oliveira et al. 2016). Yet, animals exposed to predators (Fortin et al. 2005, Tambling et al. 2015) or human-modified environments have demonstrated behavioral plasticity to varying degrees (Basille et al. 2015, Gaynor et al. 2018). For example, some species become increasingly nocturnal in areas of high human activity (Wang et al. 2015, Gaynor et al. 2018), restrict diel activity periods (Kronfeld-Schor and Dayan 2003), or physically shift their range or remain in smaller areas in sites with high livestock activity (Clark et al. 2017, Gabor and Hellgren 2000). Even subtle shifts or restrictions in activity periods might substantially increase survival probability or reduce competitive costs (Kronfeld-Schor and Dayan 2003, Frey et al. 2017), enabling species to successfully exploit human-modified environments.

Species with smaller area requirements are likely more resilient to human activity or habitat fragmentation than larger-bodied species which require greater area to persist (Henle et al. 2004, DeStefano and Deblinger 2005). However, given that most ranches are located in naturally productive landscapes, and when those are in turn embedded within a network of protected areas, such ranches may indeed support greater species diversity when compared to other modes of landscape fragmentation (Hansen et al. 2005). Thus, the predicted differences in mammal community diversity, distribution, and activity – including the responses of wider-ranging, large-bodied species – may be minimized or mitigated, resulting in less obvious or discernable changes in animal distribution or behavior. This would be in contrast to the significant differences in behavior of wildlife within landscapes which have been fragmented due to monoculture, infrastructure development (e.g., construction of dams or major roads;

Frair et al. 2008), or expansion of urbanization (McClennen et al. 2001, DeStefano and Deblinger 2005, Hansen et al. 2005, Gaynor et al. 2018).

Throughout Latin America, large-scale ranching operations are rapidly expanding to meet global demands for protein (Vera and Rivas 1997, Wassenaar et al. 2007, Aide et al. 2013, McManus et al. 2016, Armenteras et al. 2017). Within the Brazilian Pantanal, the largest inland tropical wetland in the world, more than 80% of the land surface is dedicated to intensive ranching operations and, of the remaining area (most privately held), about 5% is officially protected (Alho et al. 1988, Quigley and Crawshaw 1992, Wilcox 1992, Silva et al. 2000, Seidl et al. 2001, Tomas et al. 2019). The Pantanal is also core range for apex predators like jaguars (*Panthera onca*), and retaliatory killing for livestock losses poses a threat to long-term persistence (Quigley and Crawshaw 1992, Hoogesteijn and Hoogesteijn 2008).

Herein, I compared the spatio-temporal activity of jaguars and wild prey between a complex of strictly protected parks devoid of livestock and a complex of working ranches in the northern Brazilian Pantanal. The ranches followed “wildlife friendly” practices (Quigley et al. 2015), with no hunting or retaliatory killing of jaguar for livestock depredation. The ranches contained large herds of managed cattle (*Bos taurus*) including ~300 feral water buffalo (*Bubalus bubalis*; R. Hoogesteijn, pers. comm., Alho et al. 2011, Rosa et al. 2017), and closed to hunting for wildlife since 2009. Having both study areas closed to harvest enabled gaining insights into inherent preferences for space and resources by species within human-modified landscapes without inferences being confounded by the often uncontrolled and unknown levels of mortality risk typically accompanying such landscapes.

The objectives of this study were to (1) evaluate the temporal activity pattern and (2) spatial distribution in activity of native herbivores, jaguars, and domestic ungulates. I expected to find a constriction in activity toward – or shift to — increased nocturnality by wild prey in the ranches compared to the parks. I also anticipated that there would be a consistent overlap of jaguars and prey in the parks and ranches, meaning that jaguars likewise restricted or shifted their activity toward increased nocturnality in the ranches. In order to avoid activity overlap with humans, I expected that jaguars in the

ranches would demonstrate more concentrated activity peaks outside of the range of human activity peaks (as evidenced by cattle activity). Finally, I hypothesized that patchiness of wild species across the landscape would reflect patchiness by positively tracking with canopy cover, negatively tracking with distance from water, and negatively with distribution of domestic livestock.

## METHODS

### *Study Area*

This study was conducted in two sites under different land management practices within the northern Brazilian Pantanal (Fig. 2-1)— a region characterized by distinct dry (May-October) and wet seasons (November–April) where annual precipitation averages 1,300 mm and with nearly two-thirds of rain occurring during the wet season (Zeilhofer and Schessl 1999). The ranch (*fazenda*) study site (WGS84 S17°19'19.96", W056°44'4.20") consisted of two adjacent cattle ranches: Fazenda São Bento (275.40 km<sup>2</sup>) and Fazenda Jofre Velho (423.00 km<sup>2</sup>), which collectively contained 7,000 head of cattle during this study (R. Hoogesteijn, pers. comm.). The ranches were managed by Panthera Foundation and followed so-called “wildlife-friendly” best practices (Quigley et al. 2015), which included no hunting of native wildlife species and, in particular, did not allow killing of jaguars following livestock predation events. The purpose of this management practice was to experimentally develop alternative means of income (e.g., jaguar tourism) to offset livestock losses and facilitate jaguar persistence in multi-use landscapes (Tortato et al. 2017). Located 150 km to the west of the ranches, the park study site (WGS84 S17°49'55.23", W057°33'12.64") included two adjacent protected areas along the base of the Serra do Amolar mountain range: private reserve Acurizal (130.34 km<sup>2</sup>) and the Ramsar / UNESCO World Heritage Site, Pantanal National Park-Matogrossense (1,356.82 km<sup>2</sup>). The parks contained no livestock or agricultural operations and, in contrast to the leveed ranches, included extensive regions permanently inundated with water (Fortney et al. 2004). During this study the parks and ranches maintained similar overall densities of jaguars (*Panthera onca*; 2-4 individuals / 100 km<sup>2</sup>; Chapter 3).

Photographic surveys for analysis of wildlife activity levels were conducted using remotely-triggered digital camera traps (Pantheracam v3.0, 4.0; Panthera Foundation, NY, USA) during the dry season (June – November) in both the ranch and park sites for three years each from 2011 – 2014. Surveys spanned 40 days per site per year and were designed to photograph jaguars (Karanth and Nichols 1998; Silver et al. 2004). Initially, 42 camera traps were deployed about 40-50 cm above ground level in 21 randomly-placed stations (minimum of 2.50 km and maximum of 5.00 km apart, following recommendations in Efford 2011) in each site (Fig. 2-1). Two cameras were placed per station in order to photograph both sides of a passing animal. Off-trail stations were set within 100 m of each randomly chosen point. In order to control for potential behavioral biases in detection rates, no stations were lured or baited. The number and placement of stations was constant across years in the ranch study area but, given extreme annual flooding events in the parks, 16 and 8 stations only were repeated in the park study area in years 2 and 3, respectively. Photos were managed using Camera Trap File Manager v.2.1.9 (Panthera Foundation, NY, USA).

Each clearly visible animal was identified to the species level. For all analyses, I included only those species with > 35 independent records across the 3 seasons, with independence assumed given records  $\geq$  0.5 hr apart (O'Brien et al. 2003, Rowcliffe et al. 2014, Galetti et al. 2015; Tables 2-1, 2-B4). This yielded data on jaguar, domestic ungulates including cattle (*Bos taurus*) and feral water buffalo (Alho et al. 2011), and key native prey species (Schaller 1983) including agouti (*Dasyprocta azarae*); red and grey brocket deer (*Mazama americana* and *Mazama gouazoubira*); collared peccary (*Pecari tajacu*); white-lipped peccary (*Tayassu pecari*); and tapir (*Tapirus terrestris*). Records for red and grey brocket deer were pooled given that genetic data are required to reliably differentiate these morphologically similar species (Rossi 2000, Duarte et al. 2008).

### *Temporal Activity Patterns*

Prior to analysis, date and timestamps were extracted from each photographic record and, as we assumed that activity patterns reflected species-specific fidelity and to test response to local conditions (rather than inter-annual differences), the data were pooled over all 3 survey years for each species and study area. Time was converted from hours and minutes (24:00 hr) to radians ( $1 \text{ min time} = \frac{\pi}{720}$  radians; Table 2-B3) in order to speed up calculations and bootstrapping estimates when fitting circular kernel density curves to estimate activity patterns (Rowcliffe et al. 2014). Analyses were conducted using R software (v.3.5.1, R Core Team 2018) packages ‘activity’ (Rowcliffe et al. 2014) and ‘overlap’ (Meredith and Ridout 2018). I quantified similarity in activity patterns between jaguars, native herbivore species in the ranch and park, and cattle in the ranches using overlap coefficients following Meredith and Ridout (2018; i.e.,  $\hat{\Delta}_1$  for species with  $< 50$  samples, and  $\hat{\Delta}_4$  for species with  $> 75$  samples). Overlap coefficient values range from 0 (no overlap) to 1 (complete overlap; Ridout and Linkie 2009, Oliveira-Santos et al. 2013) and are commonly grouped into values representing low ( $< 0.50$ ), moderate ( $0.50 \leq x \leq 0.60$ ), and high ( $> 0.60$ ) degrees of overlap (Massara et al. 2018, Dias et al. 2019). Confidence intervals (95%) were estimated for overlap coefficients using 10,000 iterations of a corrected bootstrap estimator (*basic0*) and a logit distribution.

### *Spatial Activity Patterns*

I estimated a spatial activity index for all species that assumed photographic rate of capture to be representative of species-specific activity levels (not animal density or abundance) at a given location (Sollmann et al. 2013). Adapted from the framework of Jenks et al. (2011), I calculated a relative activity index ( $RA_{ctI}$ ) for each species  $i$  at site  $j$  in year  $k$  as:

$$RA_{ctI_{ijk}} = (g_i \Sigma p_{ijk} / \Sigma tn_{jk}) \times 100 \quad (1)$$

where  $g_i$  represents the average group size of species  $i$  (Table 2-1),  $\Sigma p_{ijk}$  is the sum of independent photographs, and  $\Sigma tn_{jk}$  is the sum of total trap nights (O’Brien et al. 2003). To represent the spatio-



temporal variation in predator and prey activity, the interpretation of  $RA_{ct}I$  is such that, when capturing 1 photograph of a species with an average group size of 5, and 5 photographs of a solitary species, will equate to the same overall activity levels by each species at a given site within a given user-defined timeframe (i.e., 1-hour intervals consolidated across all survey days; daily average over course of entire study period). To evaluate the degree of patchiness in spatial activity patterns,  $RA_{ct}I$  was interpolated across each study area via inverse distance weighting (Watson and Phillip 1985; see Appendix A Figs. 2-A1 and 2-A2). I sampled the smoothed  $RA_{ct}I$  values at 1,000 random points within each study area, rescaled values to range  $0 \leq x \leq 1$  for each species by dividing by the respective maximum value, and fit linear models correlating  $RA_{ct}I$  with local landscape covariates.

Landscape covariates were derived from satellite imagery to represent landscape productivity, water availability, security cover, and anthropogenic modifications (i.e., pasture; roads). Normalized difference vegetation index (NDVI; Xu et al. 2012) and normalized difference water index (NDWI; Gao 1996, McFeeters 1996) layers were derived from 28-day composites (30 m resolution) via Google Earth Engine (Gorelick et al. 2017; see code in Appendix 2-E). To capture the dynamic annual flooding regime, I processed each NDWI composite in ArcGIS v.10.3.1 (ESRI 2018) to develop layers for all intermittent and permanent water bodies in each site. At the 1,000 random points I extracted values for  $RA_{ct}I$  for each species, land cover type (i.e., pasture; ICMBio\CENAP 2010), percent canopy cover, distance from water, distance from road (truncated at 500 m), NDVI, and NDWI. Quadratic terms were included in all models for each covariate to account for potential nonlinear relationships as I expected certain relationships would not be constant (i.e.,  $RA_{ct}I$  would not follow a constant relationship with very far distances from road or river). I used the interpolated surface to depict patchiness, and the models to infer drivers of and test correlations among species.

Linear models for jaguar  $RA_{ct}I$  included  $RA_{ct}I$  values separately for individual prey species and cattle. However, given that jaguars are generalist predators, alternative models included either a single prey species or a composite wild prey covariate for  $RA_{ct}I$ . For the composite prey index, I included values

for agouti, *Dasyprocta azarae*; brocket deer, *Mazama* spp.; collared peccary, *Pecari tajacu*; tapir, *Tapirus terrestris*) — species with sufficient data (>30 independent records per species, following minimum sample size procedure as recommended in Rowcliffe et al. 2014). The relative activity of each species was rescaled to range from 0 to 1, in order to weight each species equally and allow (from the perspective of the predator) to use areas high in more than 1 prey species simultaneously. The composite prey activity metric (CAM<sub>j</sub>; similar to Schaller 1972, Galetti et al. 2009, Springer et al. 2012) was calculated as:

$$\text{CAM}_j = \sum_{i=1}^n (\text{RA}_{\text{ct}i} I_{ijk}) \quad (2)$$

All covariates were assessed for collinearity using Pearson correlation, and covariate pairs with  $r \geq 0.70$  were not included in same model (Dormann et al. 2013). All continuous covariates were centered and standardized to allow for meaningful comparison of the relative importance of each covariate. I fit full, null, and hypothesis-based models for each species using the *lm* function in program R. I tested for normality and retained only those covariates that contributed >2.00 unit change in Akaike's Information Criterion (AIC; Burnham and Anderson 2002). All models were ranked and selected by  $\Delta\text{AIC}$  and AIC weight ( $w$ ) and, where further uncertainty existed and uninformative parameters (which did not contribute > 2.00  $\Delta\text{AIC}$  change) were dropped from the model, ultimately by parsimony.

Lastly, I estimated the degree of patchiness in the  $\text{RA}_{\text{ct}i} I_{ijk}$  surfaces within the sampled study area (grain size of 0.49km<sup>2</sup>) using Moran's Index ( $I$ , interval [-1, 1]; Moran 1950),

$$I = \frac{N}{W} \times \frac{\sum_l \sum_m w_{lm} (x_l - \bar{x})(x_m - \bar{x})}{\sum_{lm} (x_l - \bar{x})^2} \quad (3)$$

where  $N$  represents the number of divisions in a region,  $W$  is the sum of all inverse distance spatial weights  $w_{lm}$ , and  $x$  and  $\bar{x}$  are the variable and variable mean for features  $l$  and  $m$ . Values of  $I$  become more dispersed as  $I$  approaches -1 and more clustered as  $I$  approaches +1. Corresponding z-scores indicate whether the spatial autocorrelation of predicted activity surfaces for species  $i$  was comprised of clusters of similar values (+ score), dissimilar values (- score; indicating potential competition between similar values), or randomly distributed due to chance alone (score ~ 0, the null expectation). Differences from

null expectations were assessed given  $\alpha = 0.05$ . All statistical analyses were conducted in programs R and ArcGIS.

## RESULTS

### *Temporal Activity Patterns*

On the ranches, a total of 1,270 independent photos of cattle, 967 of wild herbivores, 223 of feral buffalo, and 176 of jaguars were recorded over the 3 survey years (Table 2-1). Within the parks, I recorded a total of 808 independent photographs of wild herbivores and 272 of jaguars (no cattle or feral buffalo; Table 2-1). Across all species, overlap in activity patterns between the two study areas was moderate-high ( $0.62 \leq \hat{\Delta}_4 \leq 0.90$ ; Fig. 2-2). Most species, regardless of study area, exhibited minimal activity at midday except in the ranches for cattle whose activity peaked between 12:00–14:00 h (Fig. 2-2).

Collared peccary, brocket deer, feral water buffalo (ranches only) and white-lipped peccary (ranches only) remained active throughout the day, with minor peaks around sunrise and sunset (Fig. 2-2), with patterns being largely consistent between the parks and ranches for species detected in both areas ( $\hat{\Delta}_{Ranch-Park} \geq 0.85$ ). In contrast, agouti exhibited distinct crepuscular peaks in activity (~08:00 h and 18:00 h in the parks and ~06:00 h and 18:00 h in the ranches; Figs. 2-2), with a temporal shift in peaks between the 2 areas yielding a moderate coefficient of overlap ( $\hat{\Delta}_{Ranch-Park} = 0.62$ , 95% CI = 0.55-0.70). Similarly, tapirs exhibited a bimodal activity pattern (peaks ~6:00 h and 23:00 h in the parks), with a shift in peaks observed in the ranches (~01:00 and 20:00 h in the ranches;  $\hat{\Delta}_{Ranch-Park} = 0.71$ , 95% CI = 0.58-0.83; Figs. 2-2, 2-3). Among the species detected in the ranches and respective overlap with cattle (Table 2-B2), tapirs exhibited the lowest activity overlap with cattle ( $\hat{\Delta}_{Tapir-Cattle} = 0.29$ , 95% CI = 0.24-0.33; Table 2-B2).

Jaguars were active throughout the day and night and showed a trend toward increasingly crepuscular behavior in the ranches compared to the parks (Fig. 2-2), a pattern that was consistent for

both male and female jaguars (Table 2-B1). Although, jaguars exhibited high activity overlap with the composite wild herbivore activity index ( $\hat{\Delta}_4 = 0.88$ , 95% CI = 0.85-0.92), the highest overlap was observed between jaguars and brocket deer alone ( $\hat{\Delta}_4 = 0.92$  in both ranches and parks; Fig. 2-2; Table 2-B1). Moderate overlap was observed between jaguar activity and a composite of the two peccary species ( $\hat{\Delta}_4 = 0.64$ , 95% CI = 0.56-0.72; Table 2-B1). Comparatively little overlap in activity was observed between jaguars and cattle ( $\hat{\Delta}_4 = 0.44$ , 95% CI = 0.38-0.50; Fig. 2-2; Table 2-B2).

### *Spatial Activity Patterns*

The park and ranch study areas had similar overall levels of canopy cover ( $39.53\% \pm 0.37$  SE versus  $32.40\% \pm 0.20$  SE, respectively), but tree cover was patchier in the parks (Moran's  $I = 0.69$ , z-score = 69.75) than the ranches (Moran's  $I = 0.55$ , z-score = 97.56). The parks also had slightly lower productivity ( $0.47 \pm 0.004$  versus  $0.60 \pm 0.01$ ), and considerably more area close to water (average distance  $630.97 \text{ m} \pm 23.10$  SE versus  $3,506.06 \text{ m} \pm 655.06$  SE) than the ranches. Moreover, due to extreme rains and flooding during the rainy season, the parks had significantly greater water inundation in the dry season in year 3 (average distance to water =  $590.19 \text{ m} \pm 39.93$  SE) compared to year 1 (average distance to water =  $668.39 \text{ m} \pm 40.00$  SE). Within the ranches, cattle management practices intensified from years 1 through 3, with year 3 including the clearing of new pastures, construction of additional fence lines, and a ranch-wide concentration of cattle into smaller pastures in preparation for sale to slaughter (R. Hoogesteijn, pers. comm.). As a result, spatially-explicit  $RA_{ctI}$  estimates displayed substantive inter-annual shifts in distribution across both the ranches and parks for wild herbivores, domestic ungulates, and jaguars.

Across individual wild herbivore species in the ranches, the best-supported models relating  $RA_{ctI}$  to landscape covariates ( $\Delta AIC$  alternatives  $> 2.00$ ) consistently included covariates for cover, distance from water and roads, and domestic or feral herbivores (Table 2-3; Appendix C Tables 2-C1 to 2-C5; Table 2-C9). In general, wild herbivore activity was negatively related to cattle activity while positively

related to feral buffalo activity (Tables 2-C1 to 2-C5). Moran's  $I$  indicated that the activity distributions of all species were clustered in non-random patterns across the landscape (Tables 2-4, 2-5), and were generally more patchy in the ranches ( $I = 0.65-98$ ) compared to the parks ( $I = 0.48-0.71$ ). In the parks, the predictability of spatial activity patterns (as indicated by adjusted  $R^2$  values on  $RA_{ci}$  models) decreased over the 3 survey years (e.g., brocket deer  $R^2_{year1} = 0.25$ ;  $R^2_{year2} = 0.22$ ;  $R^2_{year3} = 0.11$ ; Tables 2-C1 to 2-C8), most likely due to the increasingly restrictive sampling caused by flooding. In contrast, in the ranches, adjusted  $R^2$  was relatively similar over consecutive survey years (Tables 2-4, 2-5). There was a greater range of prey activity in the parks landscape compared to the ranches, where wild herbivores ranged from 0.49 ( $< 0.01$  SE) to 0.68 ( $< 0.01$  SE) in the ranches, and from 0.50 ( $< 0.01$  SE) to 0.92 ( $< 0.01$  SE) in the parks (Table 2-6).

Jaguar activity generally increased with percent forest cover, prey activity, and water proximity (i.e., negative relationships with distance from water). Jaguar activity was higher near roads in the ranches but at intermediate distances from the roads in the parks (Table 2-C8). Notably, jaguar activity in the ranches annually varied with both positive and negative responses to activity of cattle and of the wild herbivore composite, while in the parks jaguars positively and specifically tracked with brocket deer activity (Table 2-C8). The mean activity levels for jaguars ranged more widely in the parks than in the ranches, from 0.12 ( $< 0.01$  SE) and 0.28 ( $< 0.01$  SE) in the ranches and from 0.01 ( $< 0.01$  SE) to 0.36 ( $< 0.01$  SE) in the parks (Table 2-6). The averaged predicted composite of relative activity for prey and relative activity of jaguars remained relatively stable in the ranches yet in the parks, both predator and native prey activity varied across survey years (Table 2-8).

## DISCUSSION

Within seasonally dynamic landscapes like the Pantanal, species tend to adjust spatio-temporal activity in response to the availability of habitat and food (Schaller and Crawshaw 1980, Schaller 1983, Porfirio et al. 2016). Water is a driving force of species distributions in this region, and where it is

prevalent and uncontrolled (parks) animal activity tends to be centered further from water, whereas where it is scarce and controlled (ranches), animal activity tends to concentrate near water. Anthropogenically-mediated resource availability (i.e., increased habitat fragmentation in ranches) yields more concentrated resources, which in turn results in more restricted distribution of native species distributions (e.g., prey) to those remaining patches – a pattern also found in prior studies (Desbiez et al. 2010). In contrast, environmental stochasticity (i.e., flooding regime and more extreme inundation) yielded greater variation in habitat composition and species distribution in the parks. Circadian activity patterns for some species (e.g., rodents, including species of agouti; Roll et al. 2006), however, have deep ties to physiological adaptations regardless of environmental conditions.

In this study, the temporal and spatial activity patterns of jaguar and their prey in a working ranch landscape differed subtly but meaningfully from patterns observed in nearby protected parks and reported in other regions throughout their current species distribution. Despite reduced mortality risk to wildlife given the “wildlife friendly” practices on our study ranches and, further, some degree of wildlife habituation to human activities stemming from ecotourism (Tortato et al. 2017), jaguars and their main prey exhibited less overall activity during peak levels of human activity in the ranches than in the protected areas. However, wildlife-friendly practices and jaguar ecotourism are relatively new to this region (since around 2010; Tortato et al. 2017), and over long time frames activity levels may become more synchronized with the protected areas. This is notable because, given that most ranches are located in naturally productive landscapes and when those are embedded within a network of protected areas, such ranches may indeed support greater species diversity when compared to other modes of landscape fragmentation (Hansen et al. 2005). Thus, the predicted differences in mammal community diversity, distribution, and activity – including the responses of wider-ranging, large-bodied species – may be minimized or mitigated, resulting in less obvious or discernable changes in animal distribution or behavior. This would be in contrast to the significant differences in behavior of wildlife within landscapes which have been fragmented due to monoculture, infrastructure development (e.g., construction of dams

or major roads), or expansion of urbanization (Hansen et al. 2005, Gaynor et al. 2018). Still, in this present study wild herbivore activity was concentrated in areas with low domestic cattle activity, likely due to habitat loss from forest conversion to pasture.

Investigating temporal activity patterns is useful for gaining insight into niche partitioning, species activity based on local conditions, and inter- and intraspecific interactions over time (Gray and Phan 2011, Frey et al. 2017). Trends in the activity patterns of wildlife have been assessed on a global scale, with many species shifting or restricting their activity toward nocturnality in direct response to human pressure (Gaynor et al. 2018). In contrast, within the present study animal activity levels on the ranches remained synchronized with those on protected areas. Even in the working ranchlands, jaguar activity most closely reflected the activity of wild herbivores (Azevedo et al. 2007), especially with brocket deer. Jaguars predate on over 80 different species (Foster et al. 2010), and my inclusion of a small fraction of those species – biased towards medium- and large-bodied wild herbivores that were readily detectable on cameras – likely does not reflect all the prey available to jaguars. Jaguars select prey based on relative availability or abundance across the landscape (Hayward et al. 2016), so the high degree of overlap I observed between the activity patterns of jaguar and brocket deer may reflect a greater availability of brocket deer relative to other prey species in this region. Alternatively, wild prey species exhibiting strongly crepuscular activity patterns, as exemplified by brocket deer, may be in composite the major driver of jaguar activity.

Although jaguars still preyed on livestock across the ranch landscape, spatio-temporal peaks in jaguar activity remained in synchrony with native prey. Female jaguars in the ranches, for example, had more pronounced peaks of activity around dawn and lower activity during the day, indicating potential avoidance of either cattle or the cowboys that managed the herds. Jaguars in other studies, however, killed both native wildlife and domestic livestock throughout both the day and night and tracked with prey activity patterns, indicating behavioral plasticity of jaguars to adapt to preferred prey species distribution and activity (Cavalcanti and Gese 2010). A potential implication is that, when native wild prey become

scarce (i.e., population declines due to direct persecution or limited distribution during peak dry season), predation may spill over to – or predators may exhibit prey-switching behavior onto – livestock (Sillero-Zubiri and Laurenson 2001, Loveridge et al. 2010). Evidence of such relationships between predators, wild prey availability, and prey-switching to livestock has been shown in snow leopards (*Panthera uncia*; Suryawanshi et al. 2017), wolves (*Canis lupus*; Nelson et al. 2015), and African lions (*Panthera leo*; Valeix et al. 2012). Of all documented kill sites by jaguars in the Pantanal, nearly 30% were of cattle and the remainder comprised various medium- and large-bodied native prey species (Cavalcanti and Gese 2010). Jaguars had a mean rate of about 4 days between each kill, and took one cow nearly every 25 days versus an average of wild prey species (e.g., peccary) once every 14 days (Cavalcanti and Gese 2010).

Around the world, cattle have demonstrated peaks of activity at dawn and dusk with sustained diurnal activity (Oliveira-Santos et al. 2013, Yang et al. 2018), yet in this study and in another site in the Pantanal (Azevedo et al. 2018), cattle demonstrated mostly diurnal activity with pronounced peaks around midday. Such patterns are related to activity levels of herders (Butt 2010, Zengeya et al. 2015) where, in more actively managed ranches or pastoral communities, human activity typically peaks in mid-morning, mid-afternoon (Azevedo et al. 2018), or midday (Yang et al. 2018). Cattle on ranches that are handled infrequently may naturally shift their activity to more crepuscular or nocturnal patterns – bringing with this shift increased overlap with more crepuscular periods of predator activity, and by extension, potentially increased predation risk (Muhly et al. 2011).

An important consideration is that the spatial distribution of activity levels described above are derived from an approach for relative abundance indices (RAIs). RAIs (and by association, derived estimates like relative activity) do not provide direct monotonic estimates of abundance as they lack correction for detection probabilities (Hansen et al. 2015, Sollmann et al. 2013). Namely, species with larger home ranges (e.g., jaguars) are likely more frequently photographed in a camera trap array versus species with smaller home ranges (e.g., brocket deer), therefore inflating RAI for one species while severely underestimating RAI for others (Sollmann et al. 2013). Such issues are not trivial especially



when estimates are used to guide management plans or conservation decision-making. Incorporating detection probability into relative abundance has been explored through hypothesis testing and model averaging approaches (MacKenzie and Kendall 2002). Additionally, there exist important analytical considerations for the use of relative activity indices within this present study. For example, I interpolated relative activity values across each study area, thereby creating a smoothed surface, then related these interpolated surfaces to habitat covariates – a process that may mask or modify the expected relationships between species activity and environmental conditions.

While protected areas are commonly used as adaptive baselines for species of concern, such areas are typically insufficient in size or connectivity to ensure long-term species persistence (Arcese and Sinclair 1997) and are typically designated in landscapes with lower overall productivity (Scott et al. 2001, Wittemyer et al. 2008). For example, the protected area complex in this study is one of the only regions of the Pantanal that remains permanently inundated with water throughout the year (Fortney et al. 2004) – and, in comparison to the ranches, supported fewer large-bodied wild prey (i.e., absence of white-lipped peccary). Working landscapes will continue to be a draw for wildlife including large predators (Polisar 2000, Polisar et al. 2003), especially when those working landscapes are interspersed with protected areas that may provide a source of dispersers. As demonstrated in this study, and depending upon land use and wildlife management practices, ranchlands may be functionally complementary to protected areas, (Polisar et al. 2003). However, the presence of domestic livestock and the humans who manage them will inevitably influence the distribution of native wildlife – both predators and prey – and introduce conditions ripe for human-wildlife conflict across the landscape (Kie et al. 1991, Noss 1994, Herrero et al. 2009, Inskip and Zimmermann 2009, Clark et al. 2017). The insights gained herein indicate the potential conservation value of “wildlife-friendly” working landscapes for jaguar and their prey (Quigley et al. 2015), rather than the value realized where species might not be afforded such high degrees of protection.

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Table 2-1. Key herbivore and predator species (n = 8 total) summary data (average weight in kg; average group size, number of individuals) and number of camera trap records (n) included in activity analyses for both the parks (wild species only) and ranches (wild species and domestic ungulates) over all survey years in the Brazilian Pantanal.

Common name	Scientific name	Average weight (kg)	Average group size	Ranch (n)	Park (n)	Total (n)
Agouti	<i>Dasypus novemcinctus</i>	3.00	1	214 (52.97)	190 (47.03)	404
Cattle	<i>Bos taurus</i>	175.00	10	1,270 (100.00)	0 (0.00)	1,270
Collared peccary	<i>Pecari tajacu</i>	18.00	5	38 (17.67)	177 (82.33)	215
Jaguar	<i>Panthera onca</i>	70.00	1	176 (39.29)	272 (60.71)	448
Red brocket deer,	<i>Mazama americana,</i>					
Grey brocket deer	<i>Mazama gouazoubira</i>	26.00	1	280 (41.60)	393 (58.40)	673
Tapir	<i>Tapirus terrestris</i>	150.00	1	224 (82.35)	48 (17.65)	272
Water buffalo	<i>Bubalus bubalis</i>	375.00	5	223 (100.00)	0 (0.00)	223
White-lipped peccary	<i>Tayassu pecari</i>	28.00	75	211 (100.00)	0 (0.00)	211
Native herbivores				967 (54.48)	808 (45.52)	1,775
Domestic ungulates				1,493 (100.00)	0 (0.00)	1,493
Total herbivores				2,460 (75.28)	808 (24.72)	3,268



Table 2-2. Activity peak numbers 1 (AM) and 2 (PM; 24:00 h), activity pattern (predominantly diurnal, D; nocturnal, N; crepuscular, Cr; or cathemeral, Ca), and sources for the selected wild herbivore and domestic ungulate species synthesized from literature review.

Species	Activity peak 1 (00:00—11:59 h)	Activity peak 2 (12:00—23:59 h)	Activity pattern	Source
Wild herbivore <i>Agouti spp.</i>	06:00 <sup>[2,3,7]</sup> ; 07:00 <sup>[1,4,5,8,10,12]</sup>	15:00 <sup>[5]</sup> ; 18:00 <sup>[1,2,3,4,7,8,10,12]</sup>	D <sup>[1,2,3,4,5,6,7,8,9,10,11,12]</sup>	<sup>1</sup> Gomez et al. 2005, <sup>2</sup> Lambert et al. 2009, <sup>3</sup> Norris et al. 2010, <sup>4</sup> Blake et al. 2012, <sup>5</sup> Oliveira-Santos et al. 2013, <sup>6</sup> Koster and Noss 2014, <sup>7</sup> Rowcliffe et al. 2014, <sup>8</sup> Cid et al. 2015, <sup>9</sup> Porfirio et al. 2016, <sup>10</sup> Duquette et al. 2017, <sup>11</sup> Gaynor et al. 2018, <sup>12</sup> Ferregueti et al. 2018
Brocket deer <i>spp.</i> (red clade)	02:00 <sup>[18]</sup> ; 04:00 <sup>[1,13,14,15,17]</sup> ; 05:00 <sup>[4,19]</sup> ; 06:00 <sup>[20,21]</sup> ; 07:00 <sup>[4,7,16]</sup>	15:00 <sup>[16]</sup> ; 16:00 <sup>[15,17]</sup> ; 18:00 <sup>[1,7,14,19,20]</sup> ; 19:00 <sup>[4]</sup> ; 20:00 <sup>[13,18,21]</sup>	D <sup>[7,14,16,17,21]</sup> ; N <sup>[9,13,18,19]</sup> ; Ca <sup>[1,4,15,20]</sup> ; Cr <sup>[11]</sup>	<sup>1</sup> Gomez et al. 2005, <sup>13</sup> Rivero et al. 2005, <sup>14</sup> Di Bitetti et al. 2008, <sup>15</sup> Tobler et al. 2009, <sup>16</sup> Harmsen et al. 2011, <sup>4</sup> Blake et al. 2012, <sup>17</sup> Blake et al. 2013, <sup>7</sup> Rowcliffe et al. 2014, <sup>18</sup> Ferregueti et al. 2015, <sup>19</sup> Oliveira et al. 2016, <sup>9</sup> Porfirio et al. 2016, <sup>20</sup> Pratas-Santiago et al. 2017, <sup>21</sup> Ramirez-Mejia and Sanchez 2016, <sup>11</sup> Gaynor et al. 2018
Brocket deer <i>spp.</i> (grey clade)	06:00 <sup>[13,19]</sup> ; 07:00 <sup>[18]</sup> ; 08:00 <sup>[15]</sup> ; 11:00 <sup>[4]</sup>	12:00 <sup>[22]</sup> ; 14:00 <sup>[18]</sup> ; 16:00 <sup>[15,19]</sup> ; 18:00 <sup>[4,13]</sup>	D <sup>[4,6,13,15,18,19]</sup> ; Ca <sup>[9]</sup>	<sup>13</sup> Rivero et al. 2005, <sup>15</sup> Tobler et al. 2009, <sup>4</sup> Blake et al. 2012, <sup>6</sup> Koster and Noss 2014, <sup>18</sup> Ferregueti et al. 2015, <sup>22</sup> Nanni 2015, <sup>19</sup> Oliveira et al. 2016, <sup>9</sup> Porfirio et al. 2016
Collared peccary	06:00 <sup>[5,7,23,26]</sup> ; 07:00 <sup>[17]</sup> 08:00 <sup>[1,4,15,24,25]</sup> ; 10:00 <sup>[16]</sup>	13:00 <sup>[1,15,16]</sup> ; 15:00 <sup>[4,17,25]</sup> ; 18:00 <sup>[7,24]</sup> ; 21:00 <sup>[5,23]</sup>	D <sup>[1,4,5,6,7,15,16,17,23,24]</sup> ; Ca <sup>[9]</sup> ; Cr <sup>[11]</sup>	<sup>1</sup> Gomez et al. 2005, <sup>15</sup> Tobler et al. 2009, <sup>16</sup> Harmsen et al. 2011, <sup>4</sup> Blake et al. 2012, <sup>17</sup> Blake et al. 2013, <sup>5</sup> Oliveira-Santos et al. 2013, <sup>23</sup> Cortés-Marcial and Briones-Salas 2014, <sup>6</sup> Koster and Noss 2014, <sup>7</sup> Rowcliffe et al. 2014, <sup>24</sup> Galetti et al. 2015, <sup>25</sup> Hofmann et al. 2016, <sup>9</sup> Porfirio et al. 2016, <sup>26</sup> Azevedo et al. 2018,

Tapir	01:00 <sup>[11]</sup> ; 03:00 <sup>[17,27]</sup> ; 04:00 <sup>[15,29]</sup> 06:00 <sup>[4,28]</sup>	20:00 <sup>[15]</sup> ; 21:00 <sup>[1,4,17,27]</sup> ; 22:00 <sup>[28]</sup> ; 23:00 <sup>[29]</sup>	N <sup>[1,4,5,6,9,15,17,27,28,29]</sup> ; Cr <sup>[6,11]</sup>	<sup>11</sup> Gaynor et al. 2018 <sup>27</sup> Noss et al. 2003, <sup>1</sup> Gomez et al. 2005, <sup>15</sup> Tobler et al. 2009, <sup>4</sup> Blake et al. 2012, <sup>28</sup> Wallace et al. 2012, <sup>17</sup> Blake et al. 2013, <sup>5</sup> Oliveira-Santos et al. 2013, <sup>6</sup> Koster and Noss 2014, <sup>9</sup> Porfirio et al. 2016, <sup>29</sup> Ferregueti et al. 2017, <sup>11</sup> Gaynor et al. 2018
White-lipped peccary	06:00 <sup>[24]</sup> ; 09:00 <sup>[4,15,16,17]</sup> ; 10:00 <sup>[1,5,25]</sup>	13:00 <sup>[4]</sup> ; 14:00 <sup>[5,15,17]</sup> ; 16:00 <sup>[1,16]</sup> 18:00 <sup>[24]</sup> ; 20:00 <sup>[25]</sup>	D <sup>[1,4,5,6,15,16,17,24]</sup>	<sup>1</sup> Gomez et al. 2005, <sup>15</sup> Tobler et al. 2009, <sup>16</sup> Harmsen et al. 2011, <sup>4</sup> Blake et al. 2012, <sup>17</sup> Blake et al. 2013, <sup>5</sup> Oliveira-Santos et al. 2013, <sup>6</sup> Koster and Noss 2014, <sup>24</sup> Galetti et al. 2015, <sup>25</sup> Hofmann et al. 2016
Domestic ungulate Buffalo Cattle	0:00 <sup>[30]</sup> 06:00 <sup>[32,33,35,37,38,41]</sup> ; 07:00 <sup>[5,39]</sup> ; 09:00 <sup>[40]</sup>	12:00 <sup>[30]</sup> 13:00 <sup>[31]</sup> ; 14:00 <sup>[26,34]</sup> ; 16:00 <sup>[39]</sup> ; 18:00 <sup>[32,33,35,37,38,40,41]</sup> ; 21:00 <sup>[5]</sup>	Cr <sup>[30]</sup> D <sup>[26,31,32,34,35,36,37,38,39,40,41]</sup> ; Ca <sup>[5]</sup>	<sup>30</sup> Pudyatmoko 2019 <sup>31</sup> Schlecht et al. 2004, <sup>32</sup> Aharoni et al. 2009, <sup>33</sup> Tomkins et al. 2009, <sup>34</sup> Butt 2010, <sup>35</sup> Thomas et al. 2011, <sup>36</sup> Borchard 2013, <sup>5</sup> Oliveira-Santos et al. 2013, <sup>37</sup> Dolev et al. 2014, <sup>38</sup> Perez et al. 2017, <sup>39</sup> Schoenbaum et al. 2017, <sup>40</sup> Williams et al. 2017, <sup>26</sup> Azevedo et al. 2018, <sup>41</sup> Yang et al. 2018

Table 2-3. Best-fit and null relative activity models and model selection criteria (number of parameters,  $n_{par}$ ;  $\Delta AICc$ ; AICc weight,  $w$ ) for wild herbivores (agouti; brocket deer; collared peccary; tapir; white-lipped peccary), wild predator (jaguar), and domestic herbivores (buffalo; cattle) in each study site (Ranch; Park) per survey year in the Brazilian Pantanal. Competing models included covariates for cover (percent canopy), productivity (NDVI), distance from water and road (Water dist, Road dist), and relative activity indices ( $RA_{ctI}$ ) of buffalo, cattle, composite wild herbivores ( $CAM_i$ ), and brocket deer (cumulative  $w$  of reported models  $\geq 0.80$ ). Squared terms were included to account for potential non-linearity. For best-fit model parameter estimates and ranking of top 3 models, see Appendix C Tables 2C-1 to 2C-9.

Species	Site	Year	Model	$n_{par}$	$\Delta AICc$	$w$
Agouti	Ranch	1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI}$ + $\varepsilon$	9	0	1.00
			Null	2	299.69	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle $RA_{ctI}$ + $\varepsilon$	13	0	0.57
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\varepsilon$	12	0.65	0.41
		3	Null	2	328.53	0
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI}$ + Cattle $RA_{ctI}$ + $\varepsilon$	10	0	1.00
	Park	1	Null	2	436.11	0
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\varepsilon$	12	0	1.00
		2	Null	2	644.28	0
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\varepsilon$	12	0	0.82
3	Null	2	66.06	0		
	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\varepsilon$	12	0	0.89		
Brocket deer	Ranch	1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI}$ + Cattle $RA_{ctI}$ + $\varepsilon$	10	0	1.00
			Null	2	110.40	0
	2	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI}$ + Cattle $RA_{ctI}$ + $\varepsilon$	10	0	1.00	
		Null	2	105.52	0	

			Null	2	420.60	0
	3		Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	0.99
			Null	2	410.66	0
	Park	1	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	1.00
			Null	2	275.76	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	1.00
			Null	2	239.27	0
		3	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist)) + ε	9	0	0.87
			Null	2	108.55	0
Collared peccary	Ranch	1	Buffalo RA <sub>ct</sub> I × (Road dist + Road dist <sup>2</sup> ) + ε	5	0	1.00
			Null	2	495.94	0
		2	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Null	2	272.00	0
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Null	2	947.97	0
	Park	1	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.81
			Null	2	105.29	0
		2	Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	0	0.59
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε		0.74	0.41
			Null	2	149.05	0
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + ε	8	0	0.18
			(Cover × Road dist) + Water dist + ε	6	0.45	0.14
			Cover + NDVI + (Water dist × Road dist) + ε	7	0.49	0.14
			(Cover × Road dist) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	8	1.04	0.10
			(Cover × Road dist) + NDVI + Water dist + ε	7	1.28	0.09
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	1.82	0.07
			Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	2.67	0.05
			(Cover × (Road dist + Road dist <sup>2</sup> )) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	10	3.64	0.03
			Null	2	58.49	0
Tapir	Ranch	1	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	0	1.00
			Null	2	253.83	0

		2	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Null	2	407.95	0
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Null	2	1202.91	0
	Park	1	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.93
			Null	2	147.11	0
		2	(Cover × (Road dist + Road dist <sup>2</sup> )) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	10	0	0.79
			Null	2	118.59	0
		3	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.81
			Null	2	137.31	0
White-lipped peccary	Ranch	1	(Road dist + Road dist <sup>2</sup> ) × Buffalo RA <sub>ct</sub> I + ε	5	0	1.00
			Null	2	491.14	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	0	1.00
			Null	2	314.42	0
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Null	2	758.68	0
Jaguar	Ranch	1	Cover + (Water dist + Water dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + Wild RA <sub>ct</sub> I + ε	7	0	1.00
			Null	2	273.50	0
		2	Cover + (Road dist + Road dist <sup>2</sup> ) + Wild RA <sub>ct</sub> I × (Water + Water dist <sup>2</sup> ) + ε	10	0	1.00
			Null	2	1047.49	0
		3	Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I + ε	9	0	0.99
			Null	2	357.52	0
	Park	1	Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I + ε	8	0	1.00
			Null	2	377.81	0
		2	Cover + (Water dist + Water dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I + ε	6	0	0.62
			Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I + ε	8	1.02	0.38
			Null	2	567.63	0

Buffalo	Ranch	3	Cover + (Road dist + Road dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I × (Water dist + Water dist <sup>2</sup> ) + ε	10	0	0.98
		1	Null	2	816.56	0
		1	Canopy × (Water dist + Water dist <sup>2</sup> ) + ε	5	0	0.42
		1	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	1.24	0.23
		1	Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	1.50	0.20
		1	Null	2	34.91	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	0	0.92
Cattle	Ranch	3	Null	2	241.40	0
		3	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	0	1.00
		1	Null	2	564.29	0
		1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Pasture × Road dist) + ε	9	0	0.65
		1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Pasture + ε	9	1.21	0.35
		1	Null	2	166.37	0
		2	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Pasture × Road dist) + ε	9	0	0.93
		2	Null	2	97.60	0
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Pasture × Road dist) + ε	9	0	0.78
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Pasture + ε	9	2.79	0.19
		3	Null	2	64.47	0

Table 2-4. Moran's *I* spatial autocorrelation reports and z-scores of predicted activity indices for each selected wild herbivore species (n = 4 total; all p-values < 0.01).

Species	Site	Year	Moran's <i>I</i>	z-score
Agouti	Ranch	1	0.88	27.59
		2	0.65	20.39
		3	0.93	28.91
	Park	1	0.71	25.18
		2	0.60	19.62
		3	0.49	14.60
Brocket deer	Ranch	1	0.91	28.43
		2	0.93	29.12
		3	0.90	28.14
	Park	1	0.49	17.29
		2	0.56	18.23
		3	0.60	18.00
Collared peccary	Ranch	1	0.93	29.33
		2	0.88	27.69
		3	0.98	30.60
	Park	1	0.71	25.23
		2	0.48	15.78
		3	0.50	14.89
Tapir	Ranch	1	0.81	25.48
		2	0.91	28.38
		3	0.91	28.62
	Park	1	0.50	17.65
		2	0.67	21.62
		3	0.56	16.62

Table 2-5. Moran's  $I$  spatial autocorrelation reports and z-scores of predicted composite activity indices of wild herbivores ( $CAM_i$ ) and jaguars in the parks and ranches over all survey years (all p-values < 0.01).

Species	Site	Year	Moran's $I$	z-score
$CAM_i$	Ranch	1	0.88	27.55
		2	0.92	28.86
		3	0.95	29.73
	Park	1	0.50	17.53
		2	0.68	22.06
		3	0.38	11.41
Jaguar	Ranch	1	0.97	30.13
		2	0.51	15.92
		3	0.92	28.78
	Park	1	0.76	26.92
		2	0.80	26.04
		3	0.27	8.05



Table 2-6. Annual and average predicted relative activity index ( $RA_{ctI} \pm SE$ , scaled 0:1) for composite wild herbivores ( $CAM_i$ ), jaguars, and cattle in each study site.

Group	Species	Site	Year	$RA_{ctI}$			
Wild herbivore	$CAM_i$	Ranch	1	0.13 (0.002)			
			2	0.35 (0.005)			
			3	0.48 (0.013)			
			Average	0.32 (0.005)			
			Park	1	0.65 (0.003)		
		Park	2	0.97 (<0.001)			
			3	0.55 (0.006)			
			Average	0.72 (0.002)			
			Wild predator	Jaguar	Ranch	1	0.12 (0.003)
						2	0.28 (0.001)
3	0.19 (0.004)						
Average	0.20 (0.002)						
Park	1	0.20 (0.002)					
Park	2	0.36 (0.002)					
	3	0.01 (<0.001)					
	Average	0.18 (0.001)					
	Domestic ungulate	Cattle			Ranch	1	0.19 (0.006)
						2	0.12 (0.005)
3			0.26 (0.007)				
Average			0.19 (0.004)				

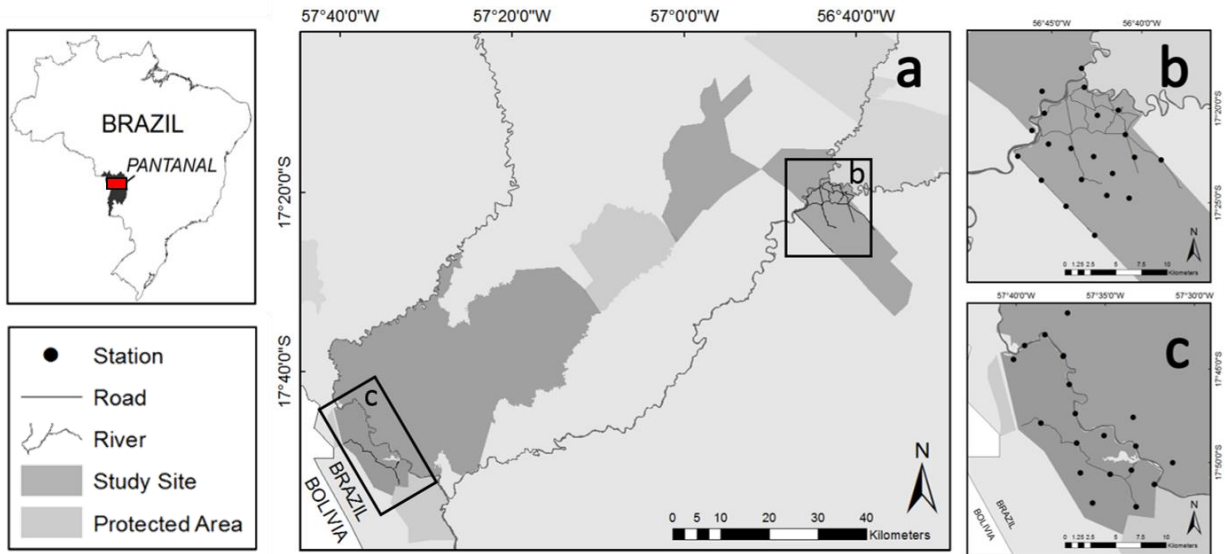


Figure 2-1. Study area (a), indicated on country map in red, located in the northern Brazilian Pantanal in states Mato Grosso (MT) and Mato Grosso do Sul (MS), with camera trap survey stations in (b) ranches (camera trap array covering 275.00 km<sup>2</sup> in Fazenda São Bento, MS and Fazenda Jofre Velho, MT) and (c) parks (camera trap array covering 300.00 km<sup>2</sup> in private reserve Acurizal, MS and Pantanal National Park-Matogrossense, MT, Brazil).

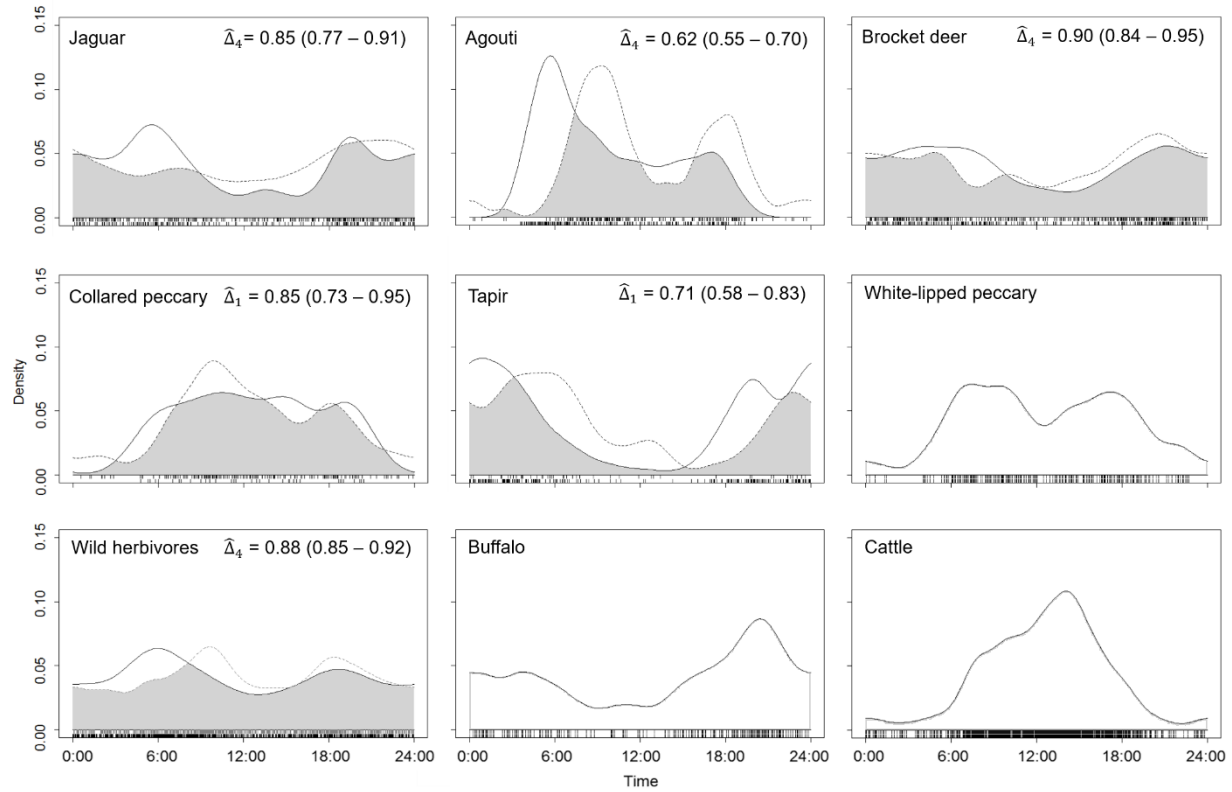


Figure 2-2. Density kernel for the temporal activity of each species in the ranches (solid line) and parks (dashed line; time in 24:00 hour format). Shaded regions indicate periods of overlap in activity between the two study areas, with the overlap estimate ( $\hat{\Delta}_1$  or  $\hat{\Delta}_4$  and 95% confidence intervals in parentheses) which quantifies the percentage of temporal activity overlap. The wild herbivore group include a composite of all wild prey species (agouti; brocket deer; collared peccary; tapir; and white-lipped peccary). No overlap estimate is given for white-lipped peccary, buffalo, or cattle, as each was only recorded in the ranches; the figures for each therefore represent daily peaks in activity patterns.

Appendix 2-A. Spatial interpolation of wild and domestic herbivore relative activity in ranches and protected areas

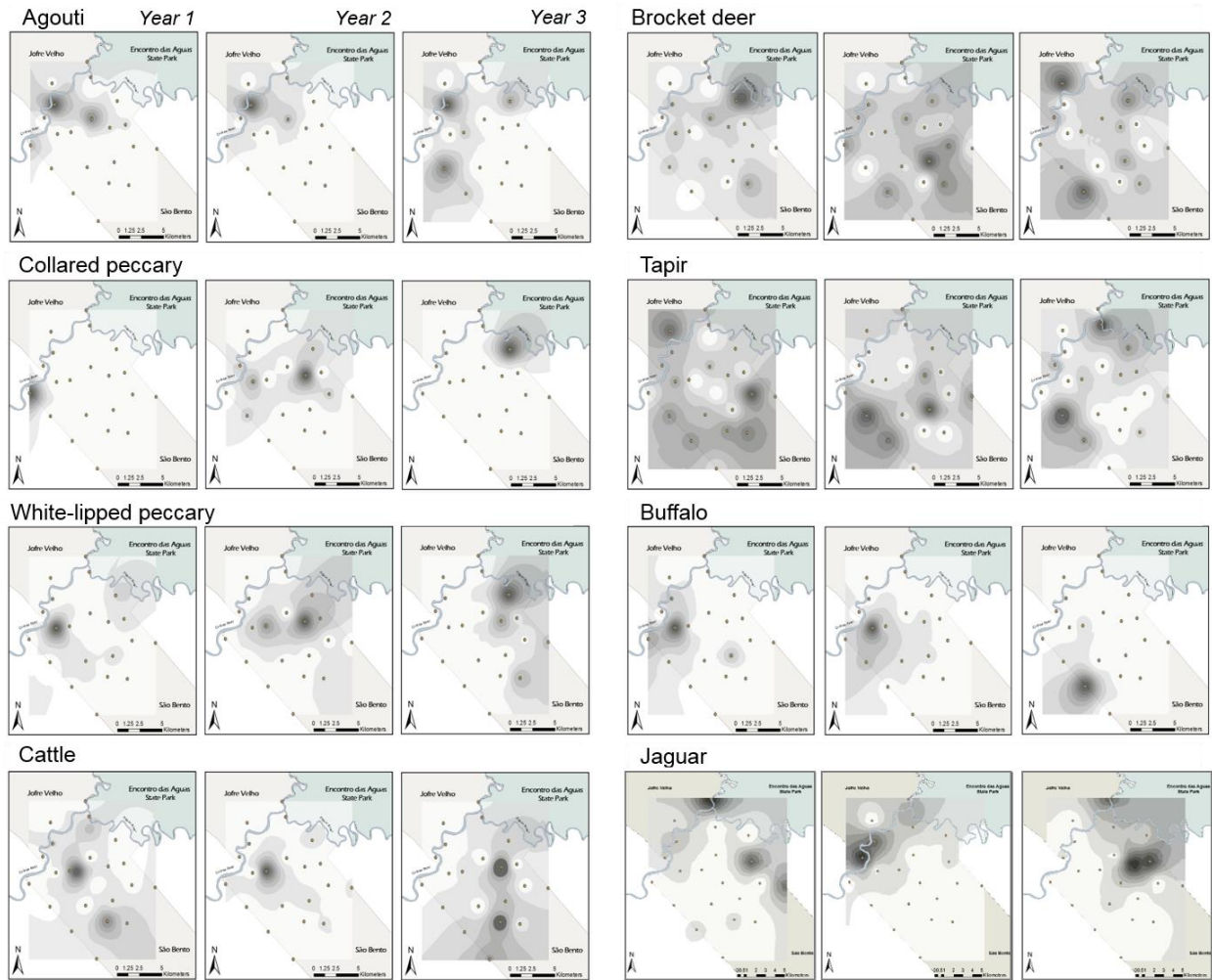


Figure 2-A1. Spatial distribution of species-specific low (light grey) to high (dark grey) activity indices interpolated via inverse distance weighting for herbivores and jaguars in the ranch for each of the 3 survey years.

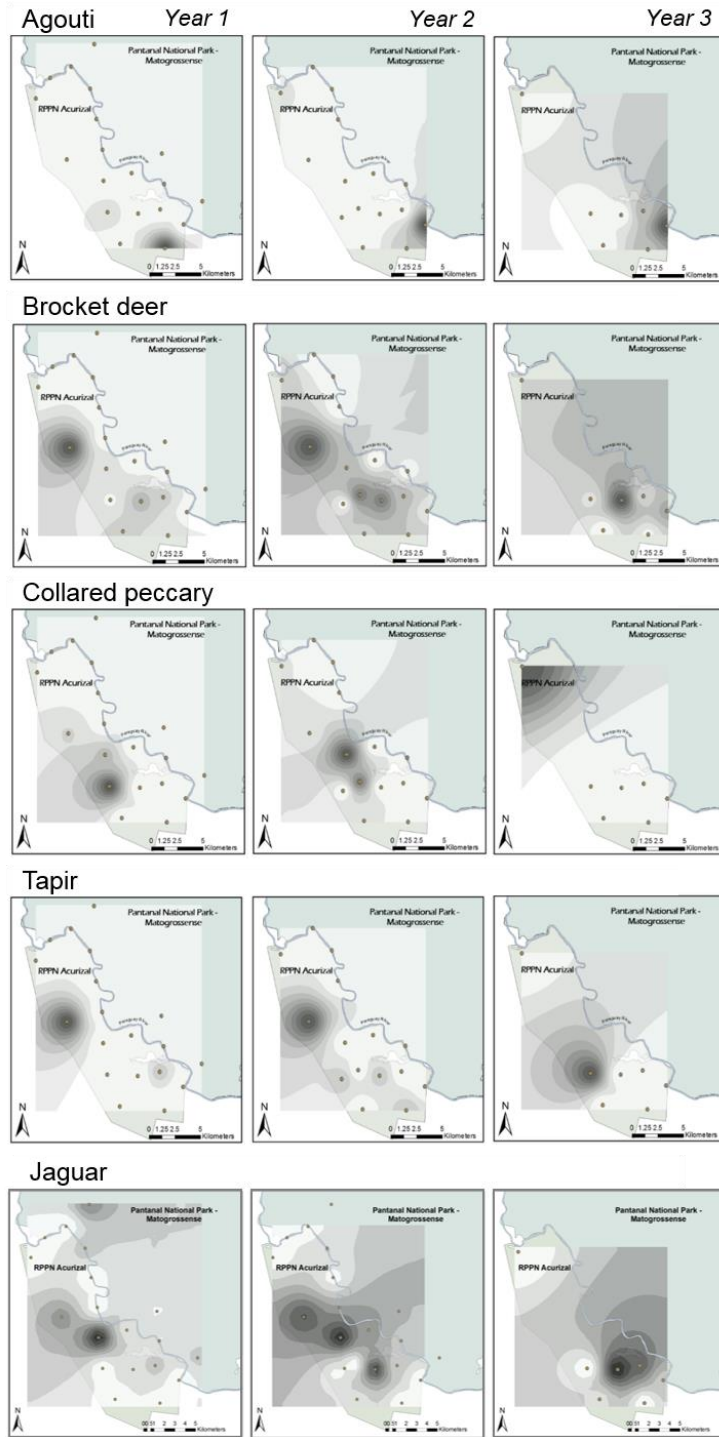


Figure 2-A2. Spatial distribution of species-specific low (light grey) to high (dark grey) activity interpolated via inverse distance weighting for wild herbivores and jaguars in the parks for each of the 3 survey years.

Appendix 2-B. Activity pattern overlap summary statistics and time intervals for wild and domestic herbivores and jaguars

Table 2-B1. Activity pattern overlap ( $\hat{\Delta}_{1,4}$ ) pairing between local populations of male and female jaguars, and between species  $i$  and jaguars in the ranch and park study sites (95% confidence intervals, CI, in parentheses).

Jaguar paired with species $i$	Site	$\hat{\Delta}_{1,4}$	95% CI	
			lower	upper
Jaguar female / Jaguar female	Ranch / Park	0.76	0.61	0.88
Jaguar male / Jaguar male	Ranch / Park	0.85	0.76	0.92
Jaguar male / Jaguar female	Ranch	0.89	0.80	0.95
Jaguar male / Jaguar female	Park	0.85	0.74	0.93
Agouti	Ranch	0.59	0.52	0.67
	Park	0.60	0.53	0.67
Brocket deer	Ranch	0.92	0.86	0.96
	Park	0.93	0.88	0.96
Collared peccary	Ranch	0.64	0.51	0.75
	Park	0.68	0.60	0.76
Tapir	Ranch	0.76	0.68	0.83
	Park	0.74	0.63	0.84
White-lipped peccary	Ranch	0.64	0.55	0.72
Pooled peccary	Ranch	0.64	0.56	0.72
Pooled wild herbivores	Ranch	0.87	0.80	0.93
	Park	0.87	0.81	0.91
Buffalo	Ranch	0.81	0.73	0.88
Cattle	Ranch	0.44	0.38	0.50

Table 2-B2. Comparative activity pattern overlap ( $\hat{\Delta}_{1,4}$ ) pairing between local populations of species  $i$  in the ranch and park study sites and cattle in the ranches (with 95% confidence intervals, CI, in parentheses).

Cattle paired with species $i$	Species $i$ site	$\hat{\Delta}_{1,4}$	95% CI	
			lower	upper
Jaguar	Ranch	0.44	0.38	0.51
	Park	0.54	0.48	0.59
Jaguar male	Ranch	0.41	0.34	0.49
	Park	0.52	0.46	0.58
Jaguar female	Ranch	0.51	0.41	0.61
	Park	0.56	0.45	0.68
Agouti	Ranch	0.64	0.57	0.70
	Park	0.69	0.62	0.74
Brocket deer	Ranch	0.49	0.44	0.55
	Park	0.49	0.44	0.53
Collared peccary	Ranch	0.78	0.66	0.88
	Park	0.79	0.72	0.85
Tapir	Ranch	0.27	0.24	0.33
	Park	0.37	0.29	0.50
White-lipped peccary	Ranch	0.75	0.69	0.81
Pooled peccary	Ranch	0.76	0.71	0.82
Pooled wild herbivores	Ranch	0.57	0.54	0.61
	Park	0.66	0.62	0.69
Buffalo	Ranch	0.45	0.40	0.52

Table 2-B3. Time intervals in 24-hour and radians for camera trap surveys conducted during the dry season (July-October). For overlap analyses, time was converted from hours and minutes to radians.

Time interval	24:00h	Radians
1	00:00–03:59	0.00–1.04
2	04:00–07:59	1.05–2.09
3	08:00–11:59	2.09–3.14
4	12:00–15:59	3.14–3.92
5	16:00–19:59	4.19–4.97
6	20:00–23:59	5.24–6.28
Sunrise (approx.)	06:00	1.57
Sunset (approx.)	18:00	4.71



Table 2-B4. Proportions of independent species records ( $\geq 30$  minutes between photographs) per time interval (24:00 h; 6 time intervals total) in the ranches and parks (July-October), and total sample size ( $n$ ) for wild herbivores (including composite, CAM<sub>i</sub> of agouti, brocket deer, collared peccary, and tapir), jaguars, and domestic ungulates.

Group	Species	Site	<i>Time interval (24:00 h)</i>						Sample ( $n$ )
			00:00 – 03:59	04:00 – 07:59	08:00 – 11:59	12:00 – 15:59	16:00 – 19:59	20:00 – 23:59	
Wild herbivore	Agouti	Ranch	0.02	0.44	0.22	0.17	0.15	0.00	214
		Park	0.03	0.13	0.40	0.11	0.28	0.05	190
	Brocket deer	Ranch	0.22	0.21	0.14	0.08	0.16	0.20	280
		Park	0.19	0.15	0.12	0.11	0.20	0.23	393
	Collared peccary	Ranch	0.00	0.21	0.26	0.29	0.16	0.08	38
		Park	0.05	0.12	0.34	0.20	0.21	0.08	177
	Tapir	Ranch	0.34	0.15	0.03	0.02	0.19	0.27	224
		Park	0.27	0.31	0.08	0.06	0.06	0.21	48
CAM <sub>i</sub>	White-lipped peccary	Ranch	0.02	0.23	0.25	0.19	0.24	0.07	211
		Ranch	0.19	0.25	0.13	0.10	0.17	0.16	756
	Park	0.13	0.15	0.23	0.13	0.21	0.15	808	
	Wild predator	Jaguar	Ranch	0.18	0.28	0.10	0.07	0.19	0.18
Park			0.18	0.13	0.12	0.12	0.21	0.25	272
Domestic ungulate	Buffalo	Ranch	0.18	0.13	0.08	0.10	0.24	0.27	223
	Cattle	Ranch	0.03	0.11	0.27	0.41	0.16	0.03	1,270

Appendix 2-C. Coefficient estimates and selection parameters for best-fit wild and domestic herbivore relative activity index models

Table 2-C1.  $\beta$  coefficient estimates (centered and standardized; standard error in parentheses) for best-fit agouti models over all survey years by study site.

Agouti	<i>Ranch</i>			<i>Park</i>		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Model covariates						
Intercept	0.108 (0.004)	0.051 (0.009)	0.153 (0.004)	0.065 (0.003)	0.080 (0.003)	0.198 (0.005)
Landscape						
% Cover (C)	-0.024 (0.004)	-0.020 (0.004)	-0.020 (0.004)	-0.019 (0.003)	-0.013 (0.004)	-0.013 (0.005)
NDVI (N)	-0.011 (0.004)	-0.007 (0.003)	-0.018 (0.004)	0.003 (0.003)	-0.008 (0.004)	-0.023 (0.005)
Road distance (R)	0.022 (0.023)	0.042 (0.024)	0.060 (0.023)	0.108 (0.021)	0.016 (0.033)	0.043 (0.057)
Road distance <sup>2</sup> (R <sup>2</sup> )	-0.049 (0.023)	-0.052 (0.023)	-0.067 (0.023)	-0.137 (0.020)	-0.036 (0.033)	-0.085 (0.058)
Water distance (W)	-0.080 (0.013)	-0.108 (0.013)	-0.091 (0.014)	0.054 (0.009)	0.014 (0.012)	-0.066 (0.016)
Water distance <sup>2</sup> (W <sup>2</sup> )	0.033 (0.013)	0.047 (0.014)	0.012 (0.014)	<0.001 (0.004)	0.008 (0.013)	0.088 (0.021)
Domestic ungulate						
Buffalo RA <sub>ct</sub> I (B)	0.034 (0.004)		0.072 (0.005)			
Cattle RA <sub>ct</sub> I (Ca)			0.018 (0.005)			
Interaction term						
W*R		-0.215 (0.082)		-0.268 (0.072)	0.047 (0.100)	0.032 (0.148)
W*R <sup>2</sup>		0.240 (0.080)		0.275 (0.070)	-0.013 (0.098)	0.014 (0.148)
W <sup>2</sup> *R		0.194 (0.094)		0.520 (0.101)	0.011 (0.178)	0.064 (0.299)
W <sup>2</sup> *R <sup>2</sup>		-0.207 (0.089)		-0.595 (0.097)	-0.119 (0.176)	-0.257 (0.305)
Adjusted R <sup>2</sup>	0.264	0.288	0.359	0.480	0.073	0.109

Table 2-C2.  $\beta$  coefficient estimates (standard error in parentheses) for brocket deer best-fit models over all survey years by study site.

Brocket deer	<i>Ranch</i>			<i>Park</i>		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Model covariates						
Intercept	0.233 (0.004)	0.417 (0.010)	0.340 (0.004)	0.172 (0.005)	0.314 (0.006)	0.339 (0.004)
Landscape						
% Cover (C)	-0.004 (0.004)	0.022 (0.004)	0.014 (0.004)	-0.005 (0.005)	-0.020 (0.006)	0.005 (0.004)
NDVI (N)	0.010 (0.004)	-0.007 (0.004)	0.034 (0.004)	-0.038 (0.005)	-0.016 (0.006)	-0.008 (0.004)
Road distance (R)	0.022 (0.025)	-0.018 (0.022)	-0.034 (0.025)	0.068 (0.037)	0.017 (0.053)	0.035 (0.009)
Road distance <sup>2</sup> (R <sup>2</sup> )	-0.037 (0.025)	0.010 (0.022)	0.050 (0.025)	-0.098 (0.036)	-0.042 (0.053)	
Water distance (W)	-0.061 (0.014)	-0.025 (0.015)	-0.071 (0.015)	0.153 (0.015)	0.150 (0.019)	-0.001 (0.013)
Water distance <sup>2</sup> (W <sup>2</sup> )	0.047 (0.014)	0.103 (0.015)	0.039 (0.015)	-0.117 (0.016)	-0.147 (0.022)	-0.064 (0.016)
Domestic ungulate						
Buffalo RA <sub>ctI</sub> (B)	-0.028 (0.004)	-0.027 (0.004)	0.085 (0.006)			
Cattle RA <sub>ctI</sub> (Ca)	-0.019 (0.004)	0.026 (0.004)	0.018 (0.005)			
Interaction term						
W×R				0.155 (0.128)	0.250 (0.162)	-0.124 (0.020)
W×R <sup>2</sup>				-0.184 (0.123)	-0.294 (0.160)	
W <sup>2</sup> ×R				-0.246 (0.178)	-0.573 (0.288)	0.263 (0.043)
W <sup>2</sup> ×R <sup>2</sup>				0.316 (0.172)	0.751 (0.286)	
Adjusted R <sup>2</sup>	0.112	0.349	0.342	0.249	0.221	0.109

Table 2-C3.  $\beta$  coefficient estimates (standard error in parentheses) for collared peccary best-fit models in all survey years in both study sites.

Collared peccary	<i>Ranch</i>			<i>Park</i>		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Model covariates						
Intercept	0.029 (0.002)	0.159 (0.009)	0.074 (0.003)	0.147 (0.005)	0.169 (0.004)	0.154 (0.006)
Landscape						
% Cover (C)		0.012 (0.003)	0.001 (0.003)	0.008 (0.006)	0.008 (0.004)	0.019 (0.007)
NDVI (N)		0.008 (0.003)	0.005 (0.003)	-0.001 (0.005)	0.010 (0.005)	0.012 (0.008)
Road distance (R)	-0.005 (0.002)	-0.030 (0.019)	0.005 (0.016)	0.008 (0.043)	0.038 (0.026)	-0.021 (0.038)
Road distance <sup>2</sup> (R <sup>2</sup> )		0.015 (0.019)	-0.017 (0.016)	-0.025 (0.041)	-0.068 (0.026)	0.043 (0.038)
Water distance (W)		0.040 (0.012)	-0.112 (0.010)	0.099 (0.017)	-0.002 (0.005)	-0.044 (0.006)
Water distance <sup>2</sup> (W <sup>2</sup> )		-0.066 (0.012)	0.076 (0.010)	-0.080 (0.018)		0.031 (0.021)
Domestic ungulate						
Buffalo RA <sub>ctI</sub> (B)	0.047 (0.002)	0.042 (0.004)	-0.077 (0.004)			
Cattle RA <sub>ctI</sub> (Ca)		-0.016 (0.003)	0.105 (0.003)			
Interaction term						
<sup>a</sup> R×B, <sup>b</sup> W×R; <sup>c</sup> C×R	-0.021 (0.002) <sup>a</sup>			0.087 (0.147) <sup>b</sup>	-0.068 (0.026) <sup>b</sup>	
W×R <sup>2</sup>				-0.014 (0.142)	-0.067 (0.037)	
W <sup>2</sup> ×R				-0.208 (0.205)		
W <sup>2</sup> ×R <sup>2</sup>				0.168 (0.197)		
Adjusted R <sup>2</sup>	0.393	0.244	0.616	0.109	0.144	0.062

Table 2-C4.  $\beta$  coefficient estimates (standard error in parentheses) for tapir best-fit models over all survey years in ranch and park study sites.

Tapir	<i>Ranch</i>			<i>Park</i>		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Model covariates						
Intercept	0.424 (0.005)	0.373 (0.013)	0.270 (0.003)	0.106 (0.005)	0.170 (0.005)	0.221 (0.007)
Landscape						
% Cover (C)	-0.012 (0.005)	0.015 (0.005)	-0.006 (0.003)	0.007 (0.005)	0.003 (0.006)	0.024 (0.006)
NDVI (N)	0.009 (0.005)	-0.030 (0.005)	-0.001 (0.003)	-0.045 (0.005)	-0.023 (0.006)	0.022 (0.007)
Road distance (R)	-0.055 (0.028)	0.021 (0.028)	0.016 (0.018)	0.034 (0.04)	0.062 (0.033)	-0.079 (0.073)
Road distance <sup>2</sup> (R <sup>2</sup> )	0.092 (0.028)	-0.019 (0.028)	-0.017 (0.018)	-0.056 (0.037)	-0.087 (0.033)	0.090 (0.075)
Water distance (W)	0.166 (0.016)	0.110 (0.018)	-0.067 (0.011)	0.095 (0.016)	0.144 (0.017)	0.113 (0.021)
Water distance <sup>2</sup> (W <sup>2</sup> )	-0.150 (0.016)	-0.055 (0.018)	-0.019 (0.010)	-0.079 (0.016)	-0.101 (0.017)	-0.115 (0.027)
Domestic ungulate						
Buffalo RA <sub>ctI</sub> (B)		0.077 (0.005)	0.036 (0.004)			
Cattle RA <sub>ctI</sub> (Ca)	-0.019 (0.005)	-0.061 (0.005)	0.118 (0.004)			
Interaction term						
<sup>a</sup> W×R, <sup>c</sup> C×R	-0.058 (0.096) <sup>a</sup>			0.354 (0.133) <sup>a</sup>	-0.009 (0.027) <sup>c</sup>	0.189 (0.192) <sup>a</sup>
<sup>b</sup> W×R <sup>2</sup> , <sup>d</sup> C×R <sup>2</sup>	0.118 (0.094) <sup>b</sup>			-0.344 (0.128) <sup>b</sup>	-0.008 (0.027) <sup>d</sup>	-0.136 (0.192) <sup>b</sup>
W <sup>2</sup> ×R	-0.012 (0.106)			-0.526 (0.185)		-0.539 (0.389)
W <sup>2</sup> ×R <sup>2</sup>	-0.082 (0.102)			0.541 (0.178)		0.588 (0.396)
Adjusted R <sup>2</sup>	0.233	0.340	0.702	0.145	0.119	0.137

Table 2-C5.  $\beta$  coefficient estimates (standard error in parentheses) for white-lipped peccary best-fit models over all survey years in ranch study site.

White-lipped peccary	<i>Ranch</i>		
	Year 1	Year 2	Year 3
Model covariates			
Intercept	0.105 (0.002)	0.159 (0.011)	0.157 (0.004)
Landscape			
% Cover (C)		0.0008 (0.004)	0.002 (0.004)
NDVI (N)		0.013 (0.004)	0.006 (0.004)
Road distance (R)	-0.002 (0.002)	0.011 (0.027)	-0.013 (0.022)
Road distance <sup>2</sup> (R <sup>2</sup> )		-0.020 (0.026)	0.0002 (0.022)
Water distance (W)		0.043 (0.015)	0.025 (0.013)
Water distance <sup>2</sup> (W <sup>2</sup> )		-0.075 (0.016)	-0.036 (0.013)
Domestic ungulate			
Buffalo RA <sub>ct</sub> I (B)	0.049 (0.002)		-0.128 (0.005)
Cattle RA <sub>ct</sub> I (Ca)			0.124 (0.005)
Interaction term			
<sup>a</sup> R×B, <sup>b</sup> W×R	0.017 (0.002) <sup>a</sup>	-0.168 (0.096) <sup>b</sup>	
W×R <sup>2</sup>		0.056 (0.093)	
W <sup>2</sup> ×R		0.228 (0.108)	
W <sup>2</sup> ×R <sup>2</sup>		-0.086 (0.104)	
Adjusted R <sup>2</sup>	0.390	0.278	0.535

Table 2-C6.  $\beta$  coefficient estimates (standard error in parentheses) for buffalo best-fit models over all survey years in ranch study site.

Buffalo	<i>Ranch</i>		
	Year 1	Year 2	Year 3
Model covariates			
Intercept	0.113 (0.004)	0.118 (0.009)	0.106 (0.004)
Landscape			
% Cover (C)	0.012 (0.005)	-0.001 (0.003)	-0.003 (0.004)
NDVI (N)		-0.016 (0.003)	-0.019 (0.004)
Road distance (R)		0.029 (0.023)	0.020 (0.023)
Road distance <sup>2</sup> (R <sup>2</sup> )		-0.031 (0.022)	-0.026 (0.023)
Water distance (W)	-0.013 (0.004)	0.082 (0.013)	0.071 (0.013)
Water distance <sup>2</sup> (W <sup>2</sup> )		-0.083 (0.013)	-0.009 (0.013)
Domestic ungulate			
Cattle RA <sub>ct</sub> I (Ca)		0.04 (0.003)	
Interaction term			
<sup>a</sup> C×W; <sup>b</sup> W×R	0.027 (0.005) <sup>a</sup>	-0.096 (0.081) <sup>b</sup>	-0.032 (0.075) <sup>b</sup>
W×R <sup>2</sup>		0.136 (0.079)	0.031 (0.075)
W <sup>2</sup> ×R		0.068 (0.092)	0.028 (0.074)
W <sup>2</sup> ×R <sup>2</sup>		-0.116 (0.088)	-0.054 (0.074)
Adjusted R <sup>2</sup>	0.037	0.223	0.437

Table 2-C7.  $\beta$  coefficient estimates (standard error in parentheses) for cattle best-fit models over all survey years in ranch study site.

Cattle	<i>Ranch</i>		
	Year 1	Year 2	Year 3
Model covariates			
Intercept	0.171 (0.004)	0.086 (0.008)	0.320 (0.006)
Landscape			
% Cover (C)	-0.008 (0.004)	-0.004 (0.003)	0.021 (0.006)
NDVI (N)	-0.018 (0.004)	-0.001 (0.003)	0.032 (0.007)
Road distance (R)	0.016 (0.004)	-0.007 (0.003)	-0.012 (0.007)
Road distance <sup>2</sup> (R <sup>2</sup> )			
Water distance (W)	0.058 (0.012)	0.045 (0.011)	0.049 (0.022)
Water distance <sup>2</sup> (W <sup>2</sup> )	-0.025 (0.012)	-0.041 (0.011)	-0.012 (0.022)
Pasture (P)	0.079 (0.037)	0.135 (0.016)	-0.017 (0.035)
Interaction term			
P×R	-0.049 (0.038)	0.036 (0.010)	-0.037 (0.021)
Adjusted R <sup>2</sup>	0.159	0.099	0.069



Table 2-C8.  $\beta$  coefficient estimates (standard error in parentheses) for jaguar best-fit linear models over all survey years in ranch and park study sites.

Jaguar	<i>Ranch</i>			<i>Park</i>		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Model covariates						
Intercept	0.167 (0.004)	0.179 (0.010)	0.195 (0.005)	0.217 (0.004)	0.354 (0.004)	0.340 (0.004)
Landscape						
% Cover (C)	-0.016 (0.004)	0.016 (0.004)	0.004 (0.005)	0.026 (0.004)	0.042 (0.005)	-0.014 (0.004)
Road distance (R)		-0.010 (0.020)	-0.081 (0.029)	0.018 (0.021)		0.037 (0.022)
Road distance <sup>2</sup> (R <sup>2</sup> )		0.024 (0.020)	0.069 (0.029)	-0.038 (0.021)		-0.048 (0.022)
Water distance (W)	-0.085 (0.014)	-0.179 (0.014)	-0.117 (0.017)	-0.029 (0.011)	-0.046 (0.013)	-0.017 (0.011)
Water distance <sup>2</sup> (W <sup>2</sup> )	0.022 (0.013)	0.076 (0.015)	0.038 (0.017)	0.018 (0.011)	0.018 (0.013)	0.006 (0.012)
Herbivore species RA <sub>ctI</sub>						
Brocket deer (Br)			-0.058 (0.005)	0.072 (0.004)	0.118 (0.004)	0.134 (0.004)
Wild herbivore (Wi)	-0.033 (0.004)	0.050 (0.005)				
Cattle (Ca)	-0.036 (0.004)		0.059 (0.005)			
Interaction term						
<sup>a</sup> W×Wi, <sup>c</sup> W×Br		-0.017 (0.014) <sup>a</sup>				-0.035 (0.010) <sup>c</sup>
<sup>b</sup> W <sup>2</sup> ×Wi, <sup>d</sup> W <sup>2</sup> ×Br		-0.020 (0.017) <sup>b</sup>				0.009 (0.009) <sup>d</sup>
Adjusted R <sup>2</sup>	0.243	0.652	0.305	0.319	0.435	0.561

Table 2-C9. Top 3 and null relative activity models and model selection criteria (number of parameters,  $npar$ ;  $\Delta AICc$ ;  $AICc$  weight,  $w$ ) for wild herbivores (agouti; brocket deer; collared peccary; tapir; white-lipped peccary), wild predator (jaguar), and domestic herbivores (buffalo; cattle) in each study site (ranch; park) per survey year. Models included covariates for cover (percent canopy), productivity (NDVI), distance from water and road (Water dist, Road dist), and relative activity indices ( $RA_{ctI}$ ) of buffalo, cattle, composite wild herbivores ( $CAM_i$ ), and brocket deer. Squared terms were included to account for potential non-linearity. For best-fit model parameter estimates, see Appendix C Tables 2C-1 to 2C-8.

Species	Site	Year	Model	$npar$	$\Delta AICc$	$w$	
<i>Wild herbivore</i>							
Agouti	Ranch	1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI} + \epsilon$	9	0	1.00	
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI} + Cattle RA_{ctI} + \epsilon$	10	1.74	0	
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\epsilon$	12	68.55	0	
			Null	2	299.69	0	
			2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle $RA_{ctI} + \epsilon$	13	0	0.57
				Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\epsilon$	12	0.66	0.41
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI} + \epsilon$	9	6.03	0.03	
			Null	2	328.53	0	
			1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI} + Cattle RA_{ctI} + \epsilon$	10	0	1.00
				Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo $RA_{ctI} + \epsilon$	9	12.18	0
				(Water dist + Water dist <sup>2</sup> ) + Buffalo $RA_{ctI} + \epsilon$	4	46.89	0
			Park	1	Null	2	436.11
	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + $\epsilon$	12			0	1.00	
	Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + $\epsilon$	9			74.85	0	

			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	89.31	0
			Null	2	644.28	0
2			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.82
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	3.14	0.17
			Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	10.69	0
			Null	2	66.06	0
3			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.89
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	4.19	0.11
			Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	13.31	0
			Null	2	105.52	0
Brocket deer	Ranch	1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	10	0	1.00
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + ε	9	17.05	0
			(Water dist + Water dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + ε	5	30.37	0
			Null	2	110.40	0
2			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	10	0	1.00
			Cover × (Road dist + Road dist <sup>2</sup> ) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	8	38.30	0
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + ε	9	38.49	0
			Null	2	420.60	0
3			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	10	0	0.99
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + ε	9	10.09	0.01
			NDVI + Buffalo RA <sub>ctI</sub> + ε	4	86.67	0
			Null	2	410.66	0
	Park	1	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	1.00
			(Cover × (Road dist + Road dist <sup>2</sup> )) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	10	15.13	0
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + ε	8	23.06	0
			Null	2	275.76	0
2			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	1.00
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	27.80	0
			(Cover × Road dist) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	10	34.32	0

Collared peccary	Ranch	3	Null	2	239.27	0		
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist) + ε	9	0	0.87		
			Cover + NDVI + (Water dist × Road dist) + ε	12	3.83	0.13		
					Water dist + (Cover × Road dist) + ε	6	31.08	0
					Null	2	108.55	0
					Buffalo RA <sub>ctI</sub> × (Road dist + Road dist <sup>2</sup> ) + ε	5	0	1.00
					Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	10	54.40	0
					Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	4	63.07	0
					Null	2	495.94	0
					Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	10	0	1.00
					Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + ε	9	20.02	0
					Buffalo RA <sub>ctI</sub> × (Water dist + Water dist <sup>2</sup> ) + ε	5	51.38	0
				Null	2	272.00	0	
				Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + Cattle RA <sub>ctI</sub> + ε	10	0	1.00	
				Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ctI</sub> + ε	4	218.57	0	
				Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ctI</sub> + ε	13	371.14	0	
				Null	2	947.97	0	
				Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.81	
				Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	2.86	0.19	
				Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	14.10	0	
				Null	2	105.29	0	
				Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	0	0.59	
				Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0.74	0.41	
				Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	13.37	0	
			Null	2	149.05	0		
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + ε	8	0	0.18		
			(Cover × Road dist) + Water dist + ε	6	0.45	0.14		
			Cover + NDVI + (Water dist × Road dist) + ε	6	0.49	0.14		
	Park	1	Null	2	947.97	0		
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.81		
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	2.86	0.19		
			Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	14.10	0		
			Null	2	105.29	0		
			Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	0	0.59		
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0.74	0.41		
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × Road dist) + ε	9	13.37	0		
			Null	2	149.05	0		
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + ε	8	0	0.18		
			(Cover × Road dist) + Water dist + ε	6	0.45	0.14		
			Cover + NDVI + (Water dist × Road dist) + ε	6	0.49	0.14		

Tapir	Ranch	1	Null	2	58.49	0
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	0	1.00
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	13.36	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist)) + ε	9	23.46	0
			Null	2	253.83	0
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + ε	9	134.40	0
			Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	4	178.25	0
			Null	2	407.95	0
	Park	1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + ε	9	79.78	0
			(Water dist + Water dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + ε	5	80.14	0
		2	Null	2	1202.91	0
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.93
			(Cover × (Road dist + Road dist <sup>2</sup> )) + NDVI + (Water dist + Water dist <sup>2</sup> ) ε	10	5.20	0.07
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + ε	8	15.60	0
			Null	2	147.11	0
			(Cover × (Road dist + Road dist <sup>2</sup> )) + NDVI + (Water dist + Water dist <sup>2</sup> ) ε	10	0	0.79
White-lipped peccary	Ranch	1	(Cover × Road dist) + NDVI + (Water dist + Water dist <sup>2</sup> ) ε	8	3.62	0.13
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	4.68	0.08
			Null	2	118.59	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + ε	12	0	0.81
			Cover + NDVI + (Water dist × (Road dist + Road dist <sup>2</sup> )) + ε	9	2.94	0.19
			(Cover × Road dist) + NDVI + (Water dist + Water dist <sup>2</sup> ) + ε	8	15.52	0
3	Null	2	137.31	0		
	(Road dist + Road dist <sup>2</sup> ) × Buffalo RA <sub>ct</sub> I + ε	5	0	1.00		
	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	46.59	0		
			NDVI + Buffalo RA <sub>ct</sub> I + ε	4	49.75	0

			Null	2	491.14	0
2			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	0	1.00
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	28.04	0
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + ε	9	49.42	0
			Null	2	314.42	0
3			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	10	0	1.00
			Buffalo RA <sub>ct</sub> I + Cattle RA <sub>ct</sub> I + ε	4	16.02	0
			Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) × (Road dist + Road dist <sup>2</sup> )) + Cattle RA <sub>ct</sub> I + ε	13	511.14	0
			Null	2	758.68	0
<i>Wild predator</i>						
Jaguar	Ranch	1	Cover + (Water dist + Water dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + Wild RA <sub>ct</sub> I + ε	7	0	1.00
			Cover + (Water dist + Water dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + Brocket deer RA <sub>ct</sub> I + ε	7	19.72	0
			Cover + (Water dist + Water dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + ε	6	51.68	0
			Null	2	273.50	0
		2	Cover + (Road dist + Road dist <sup>2</sup> ) + Wild RA <sub>ct</sub> I × (Water dist + Water dist <sup>2</sup> ) + ε	10	0	1.00
			Cover + Wild RA <sub>ct</sub> I × (Water dist + Water dist <sup>2</sup> ) + ε	8	11.70	0
			Wild RA <sub>ct</sub> I × (Water dist + Water dist <sup>2</sup> ) + ε	7	27.89	0
			Null	2	1047.49	0
		3	Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Brocket RA <sub>ct</sub> I + ε	9	0	0.99
			Cover + (Water dist + Water dist <sup>2</sup> ) + Cattle RA <sub>ct</sub> I + Brocket deer RA <sub>ct</sub> I + ε	7	8.76	0.01
			Wild RA <sub>ct</sub> I × (Water dist + Water dist <sup>2</sup> ) + ε	7	60.43	0
			Null	2	357.52	0
	Park	1	Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Brocket RA <sub>ct</sub> I + ε	8	0	1.00
			Cover + (Water dist + Water dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I + ε	6	26.06	0
			Cover + Brocket deer RA <sub>ct</sub> I + ε	4	35.99	0
			Null	2	377.81	0
		2	Cover + (Water dist + Water dist <sup>2</sup> ) + Brocket deer RA <sub>ct</sub> I + ε	4	0	0.62
			Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Brocket RA <sub>ct</sub> I + ε	5	1.02	0.38
			Cover + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Wild RA <sub>ct</sub> I + ε	3	38.28	0
			Null	2	567.63	0

		3	Cover + (Road dist + Road dist <sup>2</sup> ) + Brocket $RA_{ctI} \times (Water\ dist + Water\ dist^2) + \epsilon$	10	0	0.98
			Cover + Brocket deer $RA_{ctI} \times (Water\ dist + Water\ dist^2) + \epsilon$	8	8.24	0.02
			Brocket deer $RA_{ctI} \times (Water\ dist + Water\ dist^2) + \epsilon$	7	17.98	0
			Null	2	816.56	0
<i>Domestic herbivore</i>						
Buffalo	Ranch	1	Canopy $\times (Water\ dist + Water\ dist^2) + \epsilon$	5	0	0.42
			Canopy + NDVI + ((Water dist + Water dist <sup>2</sup> ) $\times (Road\ dist + Road\ dist^2) + \epsilon$	12	1.24	0.23
			Canopy + NDVI + (Water dist $\times (Road\ dist + Road\ dist^2) + \epsilon$	9	1.50	0.2
			Null	2	34.91	0
		2	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) $\times (Road\ dist + Road\ dist^2) + Cattle$	13	0	0.92
			$RA_{ctI} + \epsilon$			
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Cattle	9	5.63	0.06
			$RA_{ctI} + \epsilon$			
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Habitat	10	7.53	0.02
			type + Cattle $RA_{ctI} + \epsilon$			
			Null	2	241.40	0
		3	Cover + NDVI + ((Water dist + Water dist <sup>2</sup> ) $\times (Road\ dist + Road\ dist^2) + Cattle$	13	0	1.00
			$RA_{ctI} + \epsilon$			
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road dist + Road dist <sup>2</sup> ) + Cattle	9	26.88	0
			$RA_{ctI} + \epsilon$			
			(Water dist + Water dist <sup>2</sup> ) + Cattle $RA_{ctI} + \epsilon$	4	38.82	0
			Null	2	564.29	0
Cattle	Ranch	1	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Pasture $\times Road\ dist) + \epsilon$	9	0	0.65
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road + Road dist <sup>2</sup> ) + Pasture + $\epsilon$	9	1.21	0.35
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + Pasture + $\epsilon$	7	14.13	0
			Null	2	166.37	0
		2	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Pasture $\times Road\ dist) + \epsilon$	9	0	0.93
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road + Road dist <sup>2</sup> ) + Pasture + $\epsilon$	9	6.05	0.04
			(Water dist + Water dist <sup>2</sup> ) + Pasture + $\epsilon$	5	8.51	0.01
			Null	2	97.60	0
		3	Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Pasture $\times Road\ dist) + \epsilon$	9	0	0.78
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + (Road + Road dist <sup>2</sup> ) + Pasture + $\epsilon$	9	2.79	0.19
			Cover + NDVI + (Water dist + Water dist <sup>2</sup> ) + Pasture + $\epsilon$	7	6.53	0.03
			Null	2	64.47	0

## Appendix 2-D. Literature search methods and summary to establish baseline activity patterns of wild and domestic prey species

To establish baseline activity pattern synchrony throughout each species' range, I conducted a search of peer-reviewed literature on Web of Science and the first 100 most relevant results on Google Scholar (scholar.google.com, Gaynor et al. 2018). I searched titles, keywords, and abstracts for terms including activity pattern (diurnal; nocturnal; crepuscular), sampling method (e.g., camera trap; GPS telemetry), and common and scientific names for each key herbivore species (e.g., ((“*collared peccary*” OR “*Pecari tajacu*”) AND (activity OR diurnal OR nocturnal OR crepuscular OR “activity pattern” OR “time of day”) AND (telemetry OR GPS OR “camera trap” OR Neotropic\*))). I retained those articles that included hourly activity pattern analyses derived from camera trap or telemetry data for the species (or genera; Oliveira et al. 2016), or studies that classified each species as diurnal, nocturnal, crepuscular, or cathemeral based on activity pattern analysis (Noss et al. 2003, Di Bitetti et al. 2008, Tobler et al. 2009, Harmsen et al. 2011, Norris et al. 2010, Blake et al. 2012, Blake et al. 2013, Oliveira-Santos et al. 2013, Rowcliffe et al. 2014, Gaynor et al. 2018). I extracted the two peaks in circadian activity (time intervals for peak 1, 00:00—11:59 h; and peak 2, 12:00—23:59 h; as described in Aschoff 1966) and activity pattern class for each species.

The literature search returned a total of 333 candidate articles, with 41 papers meeting the requisite inclusion criteria. The assumption of intraspecific synchrony was supported whereby each species exhibited similar overall activity patterns (90.24% studies provided metrics on diurnal, crepuscular, or nocturnal activity) and activity peaks (87.80% of all studies reported activity peak metrics) throughout the respective ranges (Table 2-2). Neotropical wild herbivores had pronounced activity pattern peaks around sunrise ( $06:00 \pm 1$  h; in 80.77% of the 26 studies with wild herbivore activity peak data) and sunset ( $18:00 \pm 1$  h; in 53.85% of the 26 studies with wild herbivore activity peak data). Several wild species were primarily classified as diurnal (e.g., of the 12 agouti activity pattern studies, 100% classified



agouti as diurnal; 83.33% of 12 collared peccary studies; and 100% of 8 white-lipped peccary studies; Table 2-2), while others were considered cathemeral or nocturnal (e.g., 57.14% of 14 studies with brocket deer activity data; 83.33% of 12 studies with tapir activity data, respectively; Table 2-2). Cattle were mostly diurnal (91.67% of 12 studies with diel cattle activity data) with peak activity at sunrise and sunset (75.00% of 12 cattle studies with activity peak data), while feral buffalo were nocturnal in the single reported study (Table 2-2). In regions like the Pantanal, however, cattle had distinct peaks of activity around midday (25.00% of 12 cattle activity peak studies; Table 2-2).

Appendix 2-E. Google Earth Engine code to extract NDVI and NDWI composites developed in collaboration with Dr. Nathaniel Robinson (nathaniel.robinson@panthera.org). Additional information on the script and credits are available online at <https://code.earthengine.google.com/aefc2ba2ee1ce334e6bd078817ce6420> .

// Example Google Earth Engine code to extract NDVI and NDWI 28–day composites from Study Area.

// Create 28 day composites of NDVI for Study Area from range of years

// YYYY – YYYY (Landsat 5, Landsat 7, and Landsat 8)

// User Inputs

// Place the fusion table ID after ft:

```
var roi_fusiontable = ee.FeatureCollection('...');
```

// Place the name of the export folder

```
var export_folder = 'studyarea_NDVI';
```

// No more user inputs after this point

// Add Study Area Fusion Table

```
var studyarea = roi_fusiontable;
```

```
Map.addLayer(studyarea);
```

// Define bounds for export (Study Area), and start – end date (YYYY–MM–DD)

```
var region = studyarea.geometry();
```

```
var ls5 = ee.ImageCollection('LANDSAT/LT5_L1T_TOA')
```

```
  .filterBounds(studyarea)
```

```
  .filterDate('YYYY–MM–DD', 'YYYY–MM–DD');
```

```
var ls7 = ee.ImageCollection('LANDSAT/LE7_L1T_TOA')
```

```
  .filterBounds(studyarea)
```

```
  .filterDate('YYYY–MM–DD', 'YYYY–MM–DD');
```

```

var ls8 = ee.ImageCollection('LANDSAT/LC8_L1T_TOA')
    .filterBounds(studyarea)
    .filterDate('YYYY-MM-DD', 'YYYY-MM-DD');

// Set Cloud Mask threshold
var cloudThreshold = 20;

//Function to Mask For Clouds
function maskClouds(img){
    var sc = ee.Algorithms.Landsat.simpleCloudScore(img)
        .select(['cloud']);
    return img.mask(img.mask().and(sc.lt(cloudThreshold)));
}

// Map Cloud Mask Function over all Landsat Collections
ls5 = ls5.map(maskClouds);
ls7 = ls7.map(maskClouds);
ls8 = ls8.map(maskClouds);

// Calculate NDVI for LS5 Collection
var ls5NDVI = ls5.map(function(img){
    var ndvi = img.normalizedDifference(['B4', 'B3']);
    return(ndvi.copyProperties(img, ['system:time_start']));
});

// Scale NDVI by 1000 and cast to integer to save on export file size
ls5NDVI = ls5NDVI.map(function(img){
    return img.multiply(1000).int16().copyProperties(img, ['system:time_start']);
});

// Calculate NDVI for LS7 Collection
var ls7NDVI = ls7.map(function(img){
    var ndvi = img.normalizedDifference(['B4', 'B3']);
    return(ndvi.copyProperties(img, ['system:time_start']));
});

```

```

});

// Scale NDVI by 1000 and cast to integer to save on export file size
ls7NDVI = ls7NDVI.map(function(img){
  return img.multiply(1000).int16().copyProperties(img, ['system:time_start']);
});

// Calculate NDVI for LS8 Collection
var ls8NDVI = ls8.map(function(img){
  var ndvi = img.normalizedDifference(['B5', 'B4']);
  return(ndvi.copyProperties(img, ['system:time_start']));
});

// Scale NDVI by 1000 and cast to integer to save on export file size
ls8NDVI = ls8NDVI.map(function(img){
  return img.multiply(1000).int16().copyProperties(img, ['system:time_start']);
});

// Merge LS5 LS7 and LS8 NDVI collections
var lsNDVI = ls5NDVI.merge(ls7NDVI.merge(ls8NDVI));

// Get Start and End times in Milliseconds
var start = ee.Date('YYYY-MM-DD').millis();
print(start);
var end = ee.Date('YYYY-MM-DD').millis();
print(end);
var by = 28 × 24 × 60 × 60 × 1000;
print(by);
var dif = 14 × 24 × 60 × 60 × 1000;

// Create a feature collection with a column of dates for the Join
var pts = [];
for(var m=xxxxxxx000000; m<=xxxxxxx000000; m+=xxxxxx000000){

```

```

pts.push(
  ee.Feature(
    ee.Feature.Point([0,0]), {
      'day': m,
      'crs': 'epsg:4326'
    })
);
}

// Cast the points to a Feature Collection Object
pts = ee.FeatureCollection(pts);

// Create a Time Filter for 14 days either side of the DOY Property
var timeFilter = ee.Filter.maxDifference({
  difference: dif,
  leftField: 'day',
  rightField: 'system:time_start'
});

// Apply the Join
var lsNDVIjoin = ee.Join.saveAll('image_col').apply(pts, lsNDVI, timeFilter);

// Cast the Feature Collection Containing Image Collections to an Image Collection
var lsNDVIcol = ee.ImageCollection(lsNDVIjoin);

// Reduce Each 28 day set to the Maximum NDVI value for that 28 day period
lsNDVIcol = lsNDVIcol.map(function(f) {
  return ee.ImageCollection
    .fromImages(f.get('image_col'))
    .max()
    .set({'date':ee.Date(f.get('day'))});
});

```

```

// Rename Each Image to Include 'Year_DOY'
lsNDVIcol = lsNDVIcol.map(function(image) {
  var date = ee.Date(image.get('date'));
  var doy = date.getRelative('day', 'year');
  var year = date.format('YYYY');
  var name = ee.String(year).cat('_').cat(doy);
  var ndvi = image.select([0], [ee.String(year).cat('_').cat(doy)]);
  return (ndvi.set({'name':name}));
});

// Cast Image Collection to a list so we can loop through the collection
var lsNDVIlist = lsNDVIcol.toList(80);
print(lsNDVIlist);

/// Loop through image collection list to export individual images
/// Only export ~ 10 at a time
// for (var i = 80; i < 90; i++) {
//   Export.image(lsNDVIlist.get(i), 'NDVI_' + i,
//   {scale: 30,
//   crs: 'EPSG:4326',
//   region: region,
//   maxPixels: 3000000000000,
//   driveFolder: export_folder
//   });
// }

###END###

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## CHAPTER 3: DRIVERS OF JAGUAR (*PANTHERA ONCA*) DENSITY IN NON-HUNTED, MULTI-USE LANDSCAPES

### ABSTRACT

Protected areas serve as population strongholds for many large carnivores, with the working landscapes along their borders forming the front-line of wildlife conservation. However, understanding the dynamics of large carnivores within working landscapes is difficult where harvest is high and unregulated, as occurs across much of the range of large felids including jaguars (*Panthera onca*). This study focused on a complex of working ranches where harvest of jaguars and their prey was prohibited, to gain insight into jaguar population potential across the multi-use landscapes that dominate their range. Faced with forest fragmentation, domestic livestock subsidies, and dynamic land use practices, I expected jaguar populations in working landscapes to be predominantly male and transient, with low cub production, and with population densities inflated in remnant forest patches compared to protected areas where native forest habitat and traditional jaguar territories have been preserved. Using camera traps and spatial-capture recapture methods, I observed that male jaguars demonstrated larger-scale movements and were more detectable than females ( $0.07 \pm 0.01$  SE versus  $0.02 \pm 0.01$  SE) in both working and protected landscapes. Jaguar density increased with canopy cover and wild prey activity, decreased with domestic prey activity, and was marginally higher in the ranches ( $4.10$  individuals/100 km<sup>2</sup>  $\pm 0.07$  SE) than the parks ( $3.60$  individuals/100 km<sup>2</sup>  $\pm 0.04$  SE). Females outnumbered males in both landscapes ( $2.20$ - $2.60$  females/100 km<sup>2</sup> versus  $\sim 1.60$  males/100 km<sup>2</sup>) although local density for males reached up to  $11$  animals/100 km<sup>2</sup> in the ranches compared to a maximum of  $3.50$  males/100 km<sup>2</sup> in the parks. While overall jaguar density was patchier in the fully protected areas ( $\bar{x} = 0.69$  parks,  $0.54$  ranches), the inter-annual degree of patchiness was higher within working landscapes (Moran's  $I = 0.49$ - $0.60$  ranches,  $0.69$ - $0.70$  parks) reflecting large-scale changes in cattle management. This study demonstrated that highly modified landscapes with ongoing human disturbances can support jaguar populations on par with or exceeding that of unmodified forest habitat, provided jaguar and their native prey are also sustainably managed. Even so, effectively mitigating

jaguar-human conflict in working landscapes will be necessary to ensure connectivity among jaguar population strongholds into the future.

KEY WORDS: density; herbivore; livestock; *Panthera onca*; protected area; spatially-explicit capture-recapture; working landscape

## INTRODUCTION

Strictly protected areas are not sufficient for maintaining the world's largest terrestrial mammals (Leopold 1949, Wittemyer et al. 2008, Hansen 2011). Many parks are not adequately protected against anthropogenic perturbations, are in climatically or topographically extreme locations, or are increasingly isolated, which in turn threatens long-term viability of the wildlife dependent upon these areas (Scott et al. 2001, Wittemyer et al. 2008). Moreover, large-bodied and highly vagile mammals often require expanses of space that extend beyond park boundaries (Woodroffe and Ginsberg 1998). Although setting aside strictly protected land should remain a conservation priority, setting aside a sufficient amount of land for the world's largest animals to persist may be untenable (Hansen and Rotella 2002, Hansen and DeFries 2007, Hansen 2011). As a result, focus must necessarily shift towards making working private and public (multiple use) landscapes more wildlife friendly – in other words, increasing the functional amount of habitat between protected areas.

For many large carnivores, protected areas serve as population strongholds (Arcese and Sinclair 1997), while working landscapes along protected area borders form the front-line of conservation where human-wildlife conflict is high (Rabinowitz and Zeller 2010, Bahaa-el-din et al. 2016). Working landscapes are generally dominated by intensive or extensive agricultural, forestry, or other natural resources based economies. To meet increasing global demands for animal protein (Vera and Rivas 1996, McManus et al. 2016), conversion of closed forests to open pasture for cattle ranching is common (Wassenaar et al. 2007, Aide et al. 2013, Armenteras et al. 2017). Such landscapes are often characterized



by varying degrees of habitat loss (Devictor et al. 2008, Mortelliti et al. 2010), a patchier distribution of resources (Atmar and Patterson 1993, Hanski 1998), and often local extinction of native prey species and predators (Novaro et al. 2000, Foster et al. 2010). The extensive, varied, and nonequilibrium nature of anthropogenic land use changes hinders our ability to bring ecological theory to bear on the value of working landscapes to wildlife. Moreover, animals respond to the environment differently when under mortality risks (Lima and Dill 1990), which may obscure species' innate responses to changes in land use and thereby muddle inferences gained on the value of habitat *per se* within working landscapes. As a result, empirical study of how wild animals respond to and use working landscapes is made difficult as such landscapes typically coincide with high levels of mortality (e.g., retaliatory or pre-emptive killing of predators).

Working landscapes have long been considered population sinks (Doak 1995, Dias 1996), especially for large carnivores. Carnivores at age of dispersal may move through or be pushed into riskier habitat fragments in order to avoid direct confrontation with dominant (resident) conspecifics, contributing to ongoing conflict between predators and humans over livestock around the world (Treves and Karanth 2003, Galvez et al. 2018), especially at the border of protected areas within which predator populations may be thriving. Livestock may in fact subsidize predators, artificially elevating their densities in working landscapes (Carbone and Gittleman 2002) and perpetuating higher levels of conflict (Marchini and Macdonald 2012, Quigley et al. 2015). In the extreme condition, livestock operations might form an attractive sink (Pulliam 1988), a pernicious form of sink habitat that may be preferred over more secure source habitat and, depending on relative prevalence throughout a species' range, can drive a metapopulation to extinction (Gaona et al. 1998, Delibes et al. 2001). Importantly, studies unknowingly conducted in sink habitats may misinterpret or erroneously conclude that, due to relatively high numbers of the study species, the habitat is of high quality (Van Horne 1983, Hansen 2011). Moreover, observations of species-habitat associations in a declining population could potentially misdirect management priorities and decision-making. Yet, effective mitigation of human-wildlife conflict might

turn the working landscapes between protected areas into source habitat, or at least elevate total animal numbers to contribute more effectively to overall metapopulation stability (Naves et al. 2003, Robinson et al. 2008).

Throughout the Neotropics, human land use is the primary driver of landscape disturbance, with agriculture driving about 20% of all deforestation and large-scale cattle ranching responsible for nearly 15% of total habitat loss (Zanin et al. 2015, Armenteras et al. 2017). Wide-ranging Neotropical predators including the Near Threatened jaguar (*Panthera onca*; Quigley et al. 2017) enter into conflict with humans in these working landscapes, often due to perceived threat or actual losses due to depredation of jaguars on livestock – and jaguars are, in turn, persecuted by humans due to these perceived or actual threats (Marchini and Macdonald 2012). To understand the mechanistic responses of jaguar to cattle ranching, I examined how a ‘safe’ working landscape (where hunting of jaguar and their prey was prohibited) structured the population compared to intact, undeveloped protected areas within the Brazilian Pantanal. In this large wetland ecosystem, the most productive landscapes are used for cattle ranching while more rugged and less accessible areas have been protected (Schaller and Vasconcelos 1978). Due to this difference in biotic productivity, I expected ranchlands to support a higher diversity and density of potential prey species (despite extensive forest conversion to pasture), and by extension a higher density of jaguars, than protected parks.

Within this non-equilibrium landscape, I anticipated a breakdown in expected patterns of distribution due to provisioned domestic prey, with patches of higher jaguar densities in the ranches versus the parks. More specifically, I hypothesized that the patchier distribution of native prey and forest cover would induce more concentrated jaguar movement and patchier distribution in the working ranches compared to the parks (Weckel and Silver 2006, Azevedo and Murray 2007, Conde et al. 2010). Moreover, in contrast to the study ranches, harvest was not controlled on neighboring ranches and, as such, ranchlands were likely recognized by jaguars as riskier landscapes. I therefore expected the population of jaguars in the ranches to favor risk-tolerant males over risk-averse females (Conde et al.

2010). To gain insight into population potential within working landscapes, I compared the density and demographic composition of jaguar populations in contrasting protected and multi-use sites. Insights into acquired habitat use and population distribution of jaguars in working landscapes, independent of risk due to human-induced mortality, yields direct implications for the maintenance of jaguar connectivity and population persistence throughout their range.

## METHODS

### *Study Area*

This study was conducted in two distinct sites representing different land management practices within the northern Brazilian Pantanal (Fig. 3-1). The Pantanal is the largest inland tropical wetland on Earth (Alho et al. 1988). Encompassing an area of about 140,000 km<sup>2</sup>, this seasonally inundated floodplain includes a mosaic of riparian, semi-deciduous, and dry forest (*cerrado*) habitat (Prance and Schaller 1982, Fortney et al. 2004). The Brazilian Pantanal has distinct dry and wet seasons (May – October; November – April, respectively), and nearly two-thirds of the annual 1,300 mm precipitation falls during the wet season (Zeilhofer and Schessl 1999). About 95% of the Brazilian Pantanal is privately owned with over 80% dedicated to intensive cattle ranching operations (Quigley and Crawshaw 1992, Seidl et al. 2001).

For this study, the ranch (*fazenda*) study site (WGS84 S17°19'19.96", W056°44'4.20") consisted of two adjacent cattle ranches: Fazenda São Bento (275.40 km<sup>2</sup>) and Fazenda Jofre Velho (423.00 km<sup>2</sup>), which collectively managed ~7,000 head of cattle (R. Hoogesteijn, pers. comm.) and are managed to mitigate jaguar-human conflict (Quigley et al. 2015). The ranches followed best practices for herd management such as inclusion of naturally defensive breeds (e.g., Pantaneiro bulls) and night enclosures for young dairy calves. The ranches also prohibited hunting of native prey species or jaguars, conducted consistent surveys for livestock carcasses, and did not allow retaliatory killing of jaguars in response to predated livestock. Located 150 km to the southwest of the ranches, the park study site (WGS84

S17°49'55.23", W057°33'12.64") consisted of two adjacent protected areas along the base of the Serra do Amolar mountain range: private reserve Acurizal (130.34 km<sup>2</sup>) and the Ramsar and UNESCO World Heritage Site, Pantanal National Park-Matogrossense (1,356.82 km<sup>2</sup>). The parks contained no livestock and, in further contrast to the ranches, included extensive regions that have remained permanently inundated since a major flooding event in 1974 (Schaller and Vasconcelos 1978, Fortney et al. 2004). Worth noting is that, whereas the study areas *per se* were strictly non-hunted, unregulated harvest of wildlife occurred on the lands immediately adjacent.

### *Survey Design*

Jaguars and prey, including cattle, were monitored using motion-sensitive cameras (Karanth 1995, Karanth and Nichols 1998, Karanth et al. 2004, Silver et al. 2004, Soisalo and Cavalcanti 2006, Harmsen et al. 2010, Sollmann et al. 2011) during the dry season (June – November; 40 days/site/year) over 3 consecutive years on both the ranches and parks. I assumed demographic closure (Pradel et al. 1997, Karanth and Nichols 1998) as the surveys were limited to 40 days per year. To further meet assumptions of closure, cubs of the year that accompanied adults were not included as a jaguar detection.

In the ranches, 42 digital Pantheracams (v3.0, 4.0; Panthera Foundation, NY, USA) were deployed in 21 randomly-placed stations (spaced a minimum of 2.50 km and maximum of 5.00 km apart, following recommendations in Efford 2011). Two cameras were placed per station in order to photograph both sides of a passing jaguar. At each trail station, cameras were placed on either side of the trail while off-trail stations were set within 100 m of the original randomly chosen point. In order to control for potential behavioral biases in detection rates, no stations were lured or baited. All stations were repeatedly sampled over 3 consecutive survey years. Cameras were likewise established and monitored in the parks, but due to flood-water inundation, only 16 and 8 of the original 21 stations were repeated in years 2 and 3, respectively.

Photographic records were identified to species and (where appropriate) to individual levels, with EXIF data (date and time stamps) maintained. Photographs of  $\geq 2$  year-old jaguars (judged by body size) were identified to the individual level by referencing unique rosette patterns (Karanth and Nichols 1998, Silver et al. 2004). Male and female jaguars were distinguished whenever sexual characteristics (e.g., presence or absence of testes; distended mammary glands) were visible. I included in my analyses any herbivore species with  $\geq 30$  independent records (separated by  $\geq 30$  minutes; Rowcliffe et al. 2014). Ultimately, agouti (*Dasyprocta azarae*), brocket deer (red, *Mazama americana* and grey, *Mazama gouazoubira*), collared peccary (*Pecari tajacu*), white-lipped peccary (*Tayassu pecari*), and Brazilian tapir (*Tapirus terrestris*; Table 3-B1; Chapter 2) were included along with domestic cattle (*Bos taurus*). Although feral water buffalo (*Bubalus bubalis*) were also detected (Alho et al. 2011), I did not consider this species as prey for jaguars given the buffalo's large body size and aggressive anti-predator behaviors; indeed, buffalo are likely only available as a food resource to jaguars when jaguars scavenge carcasses (Hoogesteijn and Hoogesteijn 2008, Quigley et al. 2015).

### *Habitat and Prey Covariates*

I expected sex-specific jaguar detectability to differ between on-trail and off-trail stations (Sollmann et al. 2011), and for overall jaguar density to vary with the availability of prey and security cover (Conde et al. 2010). I mapped roads and trails using a handheld GPS unit (Garmin eTrex Legend HCx) and derived a binary variable representing 'on' ( $< 5\text{m}$ ) or 'off' ( $> 5\text{m}$ ) trail. As an index for security cover, I derived percent forest cover from a national canopy cover layer produced by the Brazilian government (ICMBio\CENAP 2010).

As an index to site productivity, the Normalized Difference Vegetation Index (NDVI; Xu et al. 2012) was derived from 28-day composites of Landsat 7 imagery (30-m resolution; Table 3-1; Chapter 2, Google Earth Engine Team 2015). Given inter-annual flood dynamics, I identified river and lagoon margins each year using the Normalized Difference Water Index (NDWI; Gao 1996, McFeeters 1996)

derived from 28-day composites with 30-m resolution (Table 3-1; Google Earth Engine Team 2015). Portions of satellite imagery interrupted by Landsat 7 band error were masked as non-habitat (< 10% of a given study site on average). As water inundation was highly variable between years, I did not use imagery from the prior year to fill in the band errors and instead used non-habitat in order to avoid introducing inaccurate water content for that particular survey year,. All GIS analyses were conducted using ArcMap v10.3.1 (ESRI 2018, Redlands, USA).

To represent prey availability, I predicted the relative activity of prey across each study area (Chapter 2; derived from Jenks et al. 2011) as:

$$\begin{aligned} \text{Domestic prey (cattle) RA}_{ct}I = & \beta_0 + (\beta_1 \times \text{distance from water}) + (\beta_2 \times \text{distance from water}^2) + \\ & (\beta_1 \times \text{distance from road}) + (\beta_2 \times \text{distance from road}^2) + (\beta_3 \times \text{NDVI}) + \\ & (\beta_5 \times \text{percent canopy cover}) + (\beta_6 \times \text{pasture}) + \varepsilon \end{aligned} \quad (1)$$

and

$$\begin{aligned} \text{Wild prey RA}_{ct}I = & \beta_0 + (\beta_1 \times \text{distance from water}) + (\beta_2 \times \text{distance from water}^2) + \\ & (\beta_2 \times \text{distance from road}) + (\beta_2 \times \text{distance from road}^2) + (\beta_3 \times \text{NDVI}) + \\ & (\beta_5 \times \text{percent canopy cover}) + (\beta_6 \times \text{feral buffalo RA}_{ct}I) + (\beta_7 \times \text{cattle RA}_{ct}I) + \varepsilon \end{aligned} \quad (2)$$

Ultimately, for each prey species I used the most parsimonious model to predict  $RA_{ct}I$  as a function of local site covariates as well as cattle and buffalo  $RA_{ct}I$  values in each landscape cell (0.49 km<sup>2</sup> resolution). Given that jaguar activity patterns significantly overlapped with brocket deer more than any other prey item (Chapter 2, Porfirio et al. 2016), I also considered models that substituted the predicted  $RA_{ct}I$  for brocket deer only in lieu of the wild prey  $RA_{ct}I$ . For prey not captured by cameras due to variable sampling distances from water, specifically caiman (*Caiman yacare*) and capybara (*Hydrochoerus hydrochaeris*), I included in models a ‘riparian zone’ variable (i.e., areas  $\leq 10$  m from rivers and lagoons = 1, otherwise 0).

### *Estimating Spatially-Explicit Density of Jaguars*

I estimated jaguar density ( $\hat{D}$ , individuals/100 km<sup>2</sup>) and detectability using spatial capture-recapture models (Borchers and Efford 2008, Royle and Young 2008, Efford et al. 2009, Efford and Fewster 2013) following the full-likelihood framework available in the program R (R Core Team 2018) package ‘secr’ (Efford 2016; for example input files and code, see Appendix 3-C). Pixel resolution (0.49 km<sup>2</sup>) was selected from a multi-scale analyses (resolution ranging from 0.10 to 5.00 km<sup>2</sup>) that identified the grain associated with maximum fit and minimal model run-time (Boyce et al. 2003). The state-space extent included a 25-km buffer around the minimum convex polygon enclosing the camera traps, yielding a total area of 3,267.39 km<sup>2</sup> in the ranch complex and 2,512.95 km<sup>2</sup> in the parks. I assumed that the probability of jaguar detection followed a half-normal distribution defined by two parameters:  $g_0$  (probability of detecting an individual given the camera trap was placed at the centroid of an activity center) and  $\sigma$  (a movement scale parameter measured in meters, defining the spread of the individual’s activity around the home range center). Home range centers were assumed to follow a Poisson distribution across both the sampled and predicted state-space. I further assumed that there was a constant probability of jaguar detection across years and study sites, but expected sex-specific differences in detectability between female and male jaguars for camera traps placed on and off roads (Sollmann et al. 2011).

I first modeled pooled jaguar density (males and females together) as a function of study site (ranch; park), wild prey RA<sub>ct</sub>I (or brocket deer RA<sub>ct</sub>I), domestic prey RA<sub>ct</sub>I, riparian zone ( $\leq 10$  m from river = 1; else 0), elevation, and forest cover (%). I estimated detection parameters as a function of survey design (camera trap placement on- or off-roads) and jaguar sex. Detection parameters were pooled across years, while density was estimated by year and site. Next, using the same set of covariates, I modeled male versus female jaguar density separately. I tested the hypotheses that male and female densities would be driven by different prevailing landscape and prey conditions – namely, that risk-averse females would concentrate in high canopy cover areas with high native prey activity, while the more risk-tolerant

males would be more evenly distributed across the landscape but should track positively with female jaguar density. Where model selection uncertainty existed for the top female models, I ran separate iterations for male models to include the female density covariate derived from the predictions of each candidate top female jaguar model.

Models were first fit to determine the need for interaction or nonlinear terms (e.g., quadratic), then multivariable models (including pairs of covariates with  $|r| < 0.70$  when  $P < 0.05$ ; Fig. 3-A1) were compared. Candidate models were ranked and selected by AIC corrected for small sample sizes (AICc; Burnham and Anderson 2002). From the top model(s), I derived a single detection parameter and year-specific density estimates for each sex in each study area. In the case of model selection uncertainty ( $\Delta\text{AICc} < 2.00$  and, where further uncertainty existed, cumulative AICc weight,  $w_i \geq 0.80$ ), predictions from the best-fit models were averaged. To quantify the degree of jaguar aggregation, or patchiness, across each landscape, I calculated Moran's  $I$  (Moran 1950) from the predicted density surfaces in each year and area using ArcGIS. The corresponding z-score indicated the likelihood that spatial patterns were random ( $-1.96 < z < 1.96$ ;  $P \geq 0.10$ ), significantly dispersed ( $z \leq -1.96$ ;  $P < 0.05$ ), or significantly clustered ( $z \geq 1.96$ ;  $P < 0.05$ ).

## RESULTS

Over the three survey years, I captured a total of 444 and 344 photographic records of jaguars in the ranches and parks, respectively (Table 3-2). Twenty-four uniquely identifiable adult jaguars were photographed in the ranches ( $n_{male} = 11$ ;  $n_{female} = 13$  individuals), and 21 in the parks ( $n_{male} = 14$ ;  $n_{female} = 7$  individuals; Table 3-2). Eleven individuals were recaptured at least once in the ranches (recapture frequency of 0.55 and 0.38 for males and females, respectively) and 8 in the parks (recapture frequency of 0.43 and 0.29 for males and females, respectively).

The top three models explaining jaguar density pooled across years included the effects of either canopy cover ( $\Delta\text{AICc} = 0.00$ ,  $w_i = 0.15$ ), cover plus cattle activity ( $\Delta\text{AICc} = 0.25$ ,  $w_i = 0.13$ ), or only wild



prey activity ( $\Delta AICc = 1.17$ ,  $w_i = 0.08$ ), although competing models included canopy cover in combination with wild prey or brocket deer activity ( $\Delta AICc = 1.27, 1.51$ , respectively; and  $w_i = 0.08, 0.07$  respectively;  $\Delta AICc$  of alternative models  $> 2.00$ ; Tables 3-3, 3-B2). Model averaged predictions of jaguar density were marginally but significantly higher in the ranches ( $4.08$  individuals /  $100 \text{ km}^2 \pm 0.07$  SE; 95% CI =  $3.94$ - $4.22$  individuals /  $100 \text{ km}^2$ ) than the parks ( $3.59$  individuals /  $100 \text{ km}^2 \pm 0.04$  SE; 95% CI =  $3.51$ - $3.67$  individuals /  $100 \text{ km}^2$ ). Male detectability was greater on versus off roads ( $0.07 \pm 0.01$  SE and  $0.05 \pm 0.01$  SE, respectively). Females were less detectable than males, though females were equally detectable both on and off roads (each estimated at  $0.02 \pm 0.01$  SE; Table 3-4). Over the study season, males moved greater distances ( $2,791.12 \text{ m} \pm 196.67$  SE) than females ( $2,193.51 \text{ m} \pm 246.08$  SE; Table 3-4). In contrast to expectations, jaguar density was patchier in the parks (Moran's  $I$  ranging from  $0.69$  to  $0.70$ ,  $p$ -value  $< 0.001$ ) than the ranches (Moran's  $I$  ranging from  $0.49$  to  $0.60$ ,  $p$ -value  $< 0.001$ ; Table 3-5), although the degree of patchiness was more variable among years on the ranches.

I then tested for sex-specific drivers of male and female jaguar density in each landscape. Due to a substantial loss of power due to subdividing the data, the null model was consistently among the top models (Table 3-B3), although in competing models and model averaged predicted estimates, some trends were observed. Sex-specific densities of jaguars were similar between the park and ranch sites with model averaged predictions of  $2.55 (\pm 0.06 \text{ SE})$  females in the ranches and  $2.16 (\pm 0.03 \text{ SE})$  females in the parks /  $100 \text{ km}^2$ , and an average of  $1.54 (\pm 0.01 \text{ SE})$  males in the ranches and  $1.57 (\pm 0.01 \text{ SE})$  males in the parks /  $100 \text{ km}^2$  (Table 3-B5). Model selection uncertainty was observed with respect to whether cover, wild prey, or no covariates drove female jaguar density (Tables 3-B3, 3-B4).

Male jaguars were more detectable than females ( $0.09 \pm 0.01$  SE versus  $0.02 \pm 0.01$  SE) in both study areas (Table 3-B5). Female jaguars moved greater distances (i.e., maintained larger ranges) in the ranches than in the parks ( $\sigma_{female,ranch} = 2,615.90 \text{ m} \pm 753.87 \text{ SE}$ ;  $\sigma_{female,park} = 790.91 \text{ m} \pm 753.87 \text{ SE}$ ), while males moved over similar distances in both sites ( $\sigma_{male,ranch} = 2,648.74 \text{ m} \pm 570.02 \text{ SE}$ ;  $\sigma_{male,park} = 2,678.96 \text{ m} \pm 836.96 \text{ SE}$ ). Drivers of male jaguar density were less certain, with the top competing models ( $\Delta AICc$

< 2.00; Table 3-B3) indicating potentially positive linear relationships with cover, brocket deer activity, and female jaguar density, but also included the null model (see Table 3-B4 for  $\beta$  coefficient estimates for top candidate models, and Table 3-B5 for model specific and model averaged predictions). Consistent with expectations, the peak jaguar density was higher in the ranches than in the parks, and the highest local densities in the ranches consisted largely of males. The predicted maximum densities of both males and females were lower in the parks (maximum density<sub>male,park</sub> = 3.50 individuals / 100 km<sup>2</sup>; maximum density<sub>female,park</sub> = 4.06 individuals / 100 km<sup>2</sup>) than in the ranches (maximum density<sub>male,ranch</sub> = 11.35 individuals / 100 km<sup>2</sup>; maximum density<sub>female,ranch</sub> = 3.85 individuals / 100 km<sup>2</sup>). Model averaged jaguar densities were more predictably clustered in the parks (female Moran's *I* range, 0.53 to 0.71; male Moran's *I* range, 0.48 to 0.70) than in the working landscapes (female Moran's *I* range, 0.38 to 0.64; male Moran's *I* range, 0.50 to 0.80; Table 3-B6).

## DISCUSSION

In this comparative study, I observed similar overall densities of jaguars between working cattle ranches where jaguars were protected from harvest and fully protected areas, indicating similar population potential. However, working ranches proved more dynamic in habitat conditions as evidenced by the degree to which jaguar density was clustered among years. Additionally, peak local densities of jaguar on the ranches were more than 3 times that observed within protected area. Jaguar activity (Chapter 2) and density (this Chapter) remained tied to native prey in the working landscapes, and tied to remnant forest patches. In fact, canopy cover was the most clear and consistent driver of jaguar density in this study.

Different from expected, I found uncertainty regarding the value of wild and domestic prey on jaguar density. This may be due in part to: (1) my reliance on relative activity rather than actual prey abundance; (2) jaguars having a generalist dietary strategy and the landscape being sufficiently productive with a variety of available prey; or (3) the fact that forest cover was the primary driver of prey activity (Chapter 2) and, therefore, was sufficient in predicting jaguar density. For prey, areas with higher cover

provide browse and security. For ambush predators like jaguars, forests provide not only security from mortality risks but also masking cover when hunting (Conde et al. 2010, Morato et al. 2018). Jaguars are generalist predators and will opportunistically consume prey they encounter and catch (Foster et al. 2010), with predation success expected to be largely contingent on spatio-temporal overlap with the greatest number of prey – meaning in the case of this study, in areas of greater canopy cover (Chapter 2). Despite considerable efforts herein to model the availability of prey items for jaguar, forest cover proved more informative – potentially providing an elegant and simple solution for predicting patterns of jaguar distribution across heterogeneous landscapes.

Comparing jaguar density in this region to the broader literature of past studies required fitting non-spatial density estimates and critiquing past and current strengths and weaknesses (Foster and Harmsen 2012, Tobler and Powell 2013). The non-spatial capture-mark-recapture estimate nearly doubled the apparent jaguar density in this region (non-spatial CR = 7.90 individuals / 100 km<sup>2</sup>; Devlin unpublished data), and yielded values comparable to some of the highest densities observed in jaguar range (i.e., in Belize, 8.80 individuals / 100 km<sup>2</sup>; Silver et al. 2004) and in other regions of the Pantanal (6.70 individuals / 100 km<sup>2</sup>; Soisalo and Cavalcanti 2006). The spatially-explicit density estimates in this study yielded lower estimates (~4.00 individuals / 100 km<sup>2</sup>) which were also more precise than non-spatial CR. Other studies on jaguars which used spatial mark-recapture analyses and compared density estimates to non-spatial CR consistently found similar trends of lower yet more precise estimates, and each study consistently recommended use of SCR over that of non-spatial CR (Sollmann et al. 2011, Noss et al. 2012, Sollmann et al. 2013, Tobler et al. 2013, Jedrzejewski et al. 2017, 2018). For example, SCR density estimates for jaguars ranged from 0.29 – 1.57 individuals / 100km<sup>2</sup> in the Brazilian Caatinga (Sollmann et al. 2011, 2013), 0.31 – 1.82 individuals / 100km<sup>2</sup> in the Bolivian Chaco (Noss et al. 2012), 4.40 individuals / 100km<sup>2</sup> in the Amazon (Tobler et al. 2013), 4.44 individuals / 100km<sup>2</sup> in the Venezuelan llanos (Jedrzejewski et al. 2017), and in a rangewide analysis, SCR estimates indicated a maximum of 9.00 individuals / 100km<sup>2</sup> (Jedrzejewski et al. 2018).

Although this study found that overall jaguar densities were comparable between the protected parks and working ranches, and both populations were significantly clustered or patchy, the degree of patchiness and variability across years were greater in the ranches. Variability was likely induced in the ranches by annual changes in herd management, which included driving cattle to different pastures, clearing forest for new pastures, and reconstructing or building new fence lines over time. In contrast, patchiness was induced in the parks largely through topography and dynamic, but generally predictable, flooding regimes. This variability in seasonal inundation due to flooding may pose a challenge in protection of livestock, as jaguar distribution tended to be less predictable depending upon changing land management practice.

Additional implications of greater patchiness in the ranches include the prevalence of higher local densities in the ranches, thereby leading to greater potential for intraspecific strife. For example, Tortato et al. (2017a) purported an increased risk of infanticide for jaguars in these ranches, as females bring cubs to large cattle carcasses where cubs are more likely to encounter unrelated conspecifics during the vulnerable time of weaning. Such antagonistic interactions can induce density-dependent consequences on proximate individual fitness (e.g., body condition), individual survival, and ultimately on local population persistence (Beckmann and Berger 2003, Johnson 2007). A similar relationship was found in a population of martens (*Martes americana*), where the frequency of territorial disputes increased with the number of territory holders, where disputes proportionately scaled with conspecific densities and increased inherent mortality risk in conspecific encounters (Fryxell et al. 1999). In the present study, I observed more jaguar cubs on camera in the ranches versus the parks. This may indicate higher cub production in the ranches, potentially offsetting the apparent cub mortality due to higher risk of infanticide in areas with patches of higher conspecific densities (Tortato et al. 2017a).

Solitary female felids defend smaller territories than males (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Grigione et al. 2002, Herfindal et al. 2005, Dillon and Kelly 2008, Goodrich et al. 2010, Conde et al. 2012) and, as with other solitary felids (Bekoff et al. 1984), male jaguars

are assumed to defend a territory large enough to contain those of 2-4 females (Schaller and Crawshaw 1980, Sunquist 1981, Sollmann et al. 2011, Rabinowitz and Nottingham 1986, Andr n 1990, Conde et al. 2010). This pattern was also observed in the Pantanal whereby female territories averaged  $69.01 \pm 28.70$  km<sup>2</sup> versus significantly larger territories secured by males ( $170.80 \pm 97.30$  km<sup>2</sup>; Cavalcanti and Gese 2010, Chapter 3). As demonstrated in prior studies (Sollmann et al. 2011), I found that jaguar movement and detectability was indeed sex-specific (Table 3-4) and that females moved over significantly shorter distances and were significantly less detectable than males (Table 3-4; Conde et al. 2010, Sollmann et al. 2011). Male felids travel over greater distances and use larger trails and roads as territorial boundaries where males can easily mark presence by depositing scats, scrapes, and scent (urine spray). Conversely, female carnivores like brown bears (*Ursus arctos*, Mace et al. 1996), black bears (*Ursus americanus*, Beckmann and Berger 2003), and tigers (*Panthera tigris*; Kerley et al. 2002) typically avoid roads – potentially as security against antagonistic encounters with males, especially when rearing vulnerable cubs.

In contrast to female jaguars in the parks, however, females in the ranches moved at significantly higher rates, indicating a possible increased pressure on females in the ranches where jaguars may need to travel over greater distances to find preferred wild prey food items – or, potentially, leaving regular home ranges to take advantage of livestock kills or carcasses. Alternatively, the significantly lower average distance from water in the parks may reflect the influence of landscape structure exerting a constraint on female movement patterns in the parks during times of cub rearing, as young cubs cannot swim across large water bodies and rivers as easily as older juveniles or females without cubs. Male jaguars were more resilient to perturbations, as shown in prior studies where male jaguars demonstrated greater risk tolerance by moving over open areas (Conde et al. 2010).

Ultimately, ranches that maintain an abundance of native prey species typically experience lower rates of cattle depredation (Roosevelt 1914, Polisar et al. 2003, Cavalcanti and Gese 2010). Many large-scale ranches, however, contribute to a decline in native prey species abundances due to clear-cutting and other forms of habitat and resource disturbance caused by the presence of cattle (Polisar et al. 2003).

Whereas individual jaguars might consume a native (smaller-bodied or < 15 kg) prey item over 1 – 2 nights and cache the carcass in a secure site, larger-bodied prey like cattle are harder to conceal and require longer handling time (e.g. ~28 hours per cow carcass on average, or a maximum of 4 days; Cavalcanti and Gese 2010). This increased handling time yields increased risk in intraspecific aggression as multiple individuals may concentrate on a single cattle carcass (Rampim et al. *in prep*) or may drive greater social tolerance among otherwise solitary conspecific predators like pumas (*Puma concolor*; Pierce et al. 2011, Elbroch et al. 2017).

The potential exists for working ranches located in more productive landscapes to maintain diverse prey despite forest reduction. Given sufficient protection from hunting or human retaliation, such multi-use areas can yield populations on par with protected areas – indicating that, perhaps, absolute protection is not necessary so long as there is sufficient forest habitat. Further, habitat amount is more important than arrangement, and where space and prey are sufficient, as was the case in this study, jaguar habitat might simply be inferred by the amount of forest cover – important especially for recently modified Brazilian Forest Code legislation (Lei 12.651, 2012) that decrees 50% forest cover must be maintained per ranch (in contrast to prior 1965 code Lei 4.771). The ranches surveyed in this study followed the mosaic model of conservation and included a variety of multi-use landscapes (working and protected landscapes; Quigley et al. 2015), including support for a local school and a lucrative local ecotourism economy to offset financial losses due to livestock predation by jaguar (Tortato et al. 2017b).

The advantage of the present study was in its comparisons, whereby the protected park providing a baseline for jaguar population potential in the working landscape, and the fact that harvest was prohibited in both landscapes enabling more robust inference into the inherent responses of jaguar to land use changes associated with livestock ranching. Such pressures are already observed in tiger range where cases of human-wildlife conflict are increasing as tiger populations recover within protected areas and expand into adjacent working landscapes (Bargali and Ahmed 2018, Neelakantan et al. 2019). For jaguars, our study indicates that conservation efforts should continue to focus on the protection of security

cover and native prey base – the main drivers of predator density – to most effectively support the long-term persistence of resident female (and, consequently, resident male) jaguar populations.

Conservation must inevitably embrace an integrated approach of studying and managing species in a mosaic of protected, private, and public land use areas (Crawshaw 2003). While protected areas provide strongholds for wildlife, they are not sufficiently large to sustain long-term metapopulation persistence. As noted by Leopold (1949) in an era during which large carnivores were actively extirpated from parks, “Even the national parks, which run up to a million acres each in size, have not been large enough to retain natural predators...” More recently, Woodroffe and Ginsberg (1998) found that human-wildlife conflict around protected area borders occurs at such high rates that populations of wide-ranging carnivores are likely to face extinction, especially when those populations reside in isolated parks. Understanding the habitat requirements and population potential for free-ranging animals across multiple use landscapes is constrained by prior studies having been conducted solely in protected areas (Silver et al. 2004, Weckel et al. 2006, Conde et al. 2010, Harmsen et al. 2011, Sollmann et al. 2011) or solely conducted in human-modified landscapes where both predators and prey were subject to often uncontrolled and unknown levels of harvest pressure (Gutierrez-Gonzalez et al. 2015).

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Table 3-1. Comparative average values ( $\pm$  SE) of habitat quality covariates in each study site (park; ranch) in the northern Brazilian Pantanal, including: distance from water (m); elevation (m); NDVI; and canopy cover (%).

Site	Distance from water (m)	Elevation (m)	NDVI	Cover (%)
Park	279.75 (40.88)	126.00 (1.32)	0.47 (0.004)	39.53 (0.37)
Ranch	3,506.06 (655.06)	110.65 (0.05)	0.60 (0.01)	32.40 (0.20)

Table 3-2. Survey effort, total number of records (jaguar photos), and total number of photographed female, male, and unknown individuals (percentages in parentheses) over all 3 survey years (2011 – 2014) in each study area (park; ranch) in the Brazilian Pantanal.

Site	Effort (trap nights)	Records	Adult females	Adult males	Unknown	Total adults
Park	3,378 (47.03)	344 (43.65)	7 (35.00)	14 (51.85)	7 (50.00)	28 (47.46)
Ranch	3,804 (52.97)	444 (56.35)	13 (65.00)	11 (40.74)	7 (50.00)	31 (52.54)
Total	7,182	788	20	27	14	59

Table 3-3. Top candidate ( $\Delta\text{AICc} < 2.00$ ) and null spatially-explicit capture-recapture models for jaguars in a ranch and protected area complex in the northern Brazilian Pantanal, wherein model reports include covariates for density ( $D$ ), sex-specific ( $h_2$ ) detection parameters ( $g_0$ ;  $\sigma$ ), number of parameters ( $npar$ ), and selection criteria ( $\Delta\text{AICc}$ ; AICc weight,  $w$ ).

Model	$npar$	$\Delta\text{AICc}$	$w$
$D \sim (\text{Cover}), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	9	0	0.15
$D \sim (\text{Cover} + \text{Cattle } RA_{ctI}), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	10	0.25	0.13
$D \sim (\text{Wild prey } RA_{ctI}), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	9	1.17	0.08
$D \sim (\text{Cover} + \text{Brocket deer } RA_{ctI}), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	10	1.27	0.08
$D \sim (\text{Cover} + \text{Wild prey } RA_{ctI}), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	10	1.51	0.07
$D \sim (\text{Cover} + \text{Brocket deer } RA_{ctI} + \text{Cattle } RA_{ctI}), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	11	1.97	0.05
Null hypothesis, $D \sim (1), g_0 \sim (h_2 \times \text{Roads}), \sigma \sim (h_2)$	8	3.17	0.03
Full null model, $D \sim (1), g_0 \sim (1), \sigma \sim (1)$	4	39.32	0

Table 3-4. Site-specific density (individuals / 100 km<sup>2</sup>) and sex-specific detection ( $g0$ ;  $\sigma$ , in meters) parameter estimates ( $\pm$  SE) of the selected best-fit models (top 3) and model average estimates for jaguars in a ranch and protected area complex in the northern Brazilian Pantanal.

Model	<i>Density</i>		<i>g0</i>		<i>σ</i>
	Ranch	Parks	On road	Off road	(.)
<i>D~(Cover), g0~(h2 × Roads), σ~(h2)</i>					
Males			0.03 (0.01)	0.05 (0.01)	2,754.87 (185.23)
Females	3.98 (0.07)	3.50 (0.04)	0.01 (0.003)	0.02 (0.01)	2,171.57 (239.69)
<i>D~(Cover + Cattle RA<sub>ctI</sub>), g0~(h2 × Roads), σ~(h2)</i>					
Males			0.09 (0.01)	0.05 (0.01)	2,740.36 (182.30)
Females	4.15 (0.07)	3.51 (0.03)	0.02 (0.01)	0.03 (0.01)	2,192.14 (242.88)
<i>D~(Wild prey RA<sub>ctI</sub>), g0~(h2 × Roads), σ~(h2)</i>					
Males			0.09 (0.01)	0.05 (0.01)	2,935.98 (239.80)
Females	4.17 (0.07)	3.88 (0.05)	0.02 (0.01)	0.02 (0.01)	2,235.01 (262.58)
Model average					
Males			0.07 (0.01)	0.05 (0.01)	2,791.12 (196.67)
Females	4.08 (0.07)	3.59 (0.04)	0.02 (0.02)	0.02 (0.01)	2,193.51 (246.08)

Table 3-5. Moran's index ( $I$ , z-score in parentheses; all  $p$ -values < 0.05) for annual density surfaces predicted from selected best-fit models and model averages for jaguars in a protected area and ranch complex in the northern Brazilian Pantanal.

Model	<i>Ranch</i>			<i>Park</i>		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
$D \sim (\text{Cover}), g0 \sim (h2 \times \text{Roads}), \sigma \sim (h2)$	0.53 (84.75)	0.51 (81.08)	0.56 (71.43)	0.71 (71.76)	0.71 (71.76)	0.71 (71.76)
$D \sim (\text{Cover} + \text{Cattle } RA_{ct}I), g0 \sim (h2 \times \text{Roads}), \sigma \sim (h2)$	0.49 (78.35)	0.53 (82.79)	0.55 (69.20)	0.71 (71.62)	0.71 (71.62)	0.71 (71.62)
$D \sim (\text{Wild prey } RA_{ct}I), g0 \sim (h2 \times \text{Roads}), \sigma \sim (h2)$	0.53 (84.85)	0.40 (62.56)	0.92 (116.63)	0.73 (74.39)	0.71 (71.94)	0.60 (62.60)
Model average	0.52 (82.61)	0.49 (77.88)	0.60 (75.61)	0.69 (69.84)	0.70 (70.83)	0.69 (70.27)

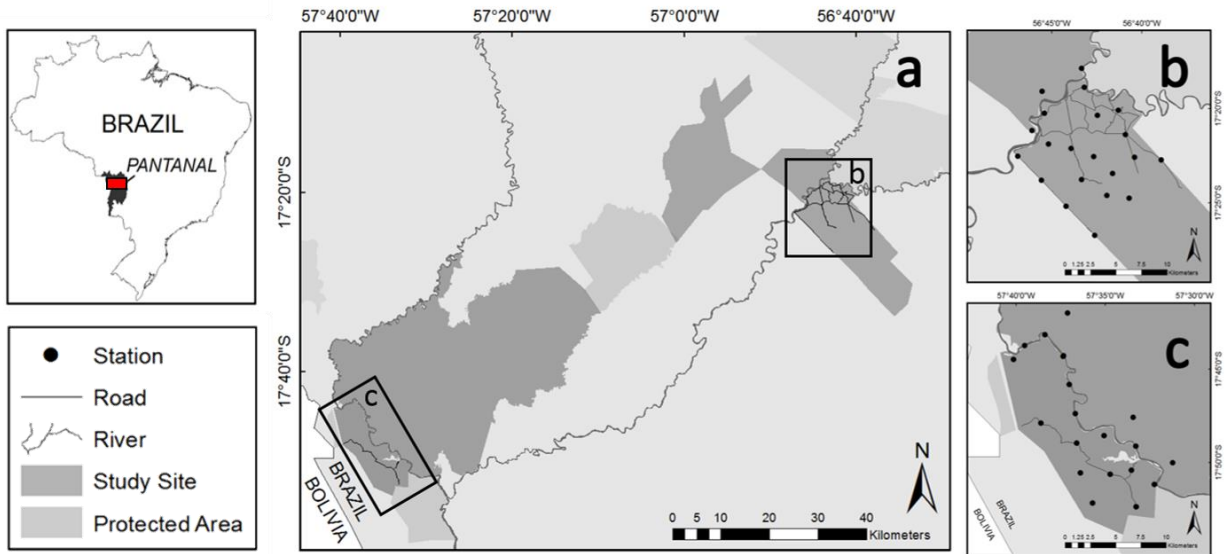


Figure 3-1. Study area (a), indicated on country map in red, located in the northern Brazilian Pantanal in states Mato Grosso (MT) and Mato Grosso do Sul (MS), with camera trap survey stations in (b) ranches (camera trap array covering 275.00 km<sup>2</sup> in Fazenda São Bento, MS and Fazenda Jofre Velho, MT) and (c) parks (camera trap array covering 300.00 km<sup>2</sup> in private reserve Acurizal, MS and Pantanal National Park-Matogrossense, MT, Brazil).



Appendix 3-A. Multicollinearity tests for model covariates

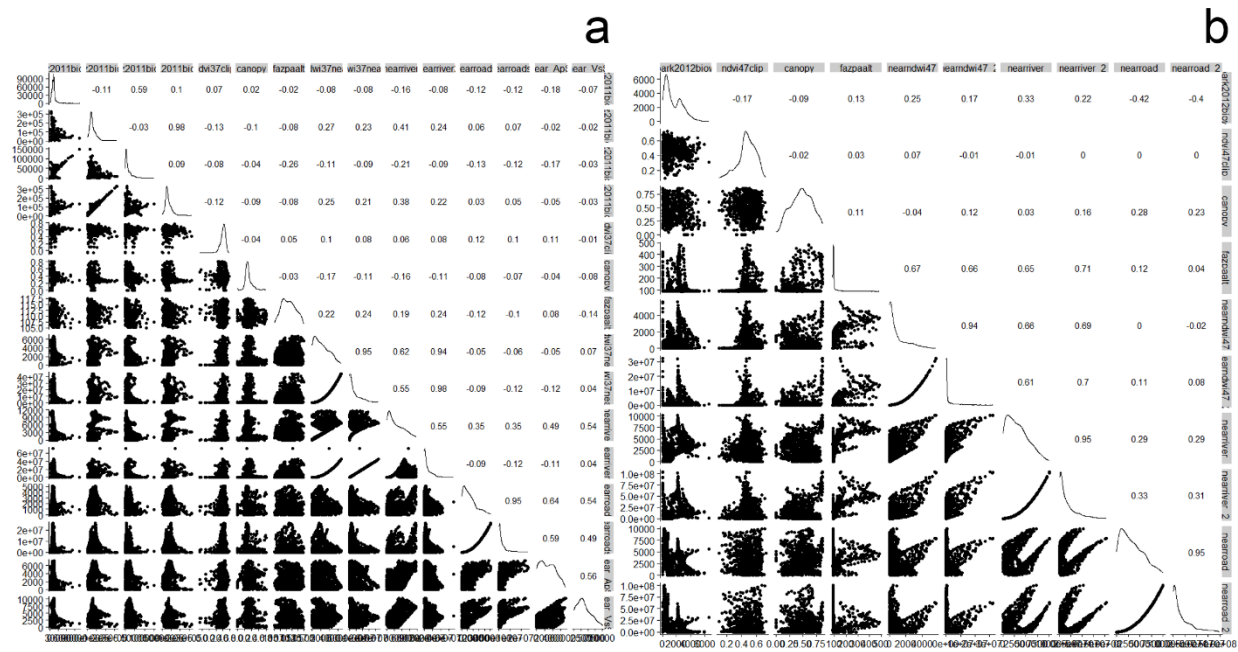


Figure 3-A1. Model covariates were tested for multicollinearity using Pearson’s correlation, with an example correlation matrix for ranch (a) and park (b) covariates for percent cover, elevation, NDWI, and NDVI. Any covariates with correlation values of  $|r| \geq 0.70$  were not included in the same model.

Appendix 3-B. Tables and figures of spatially-explicit capture-recapture covariates and model results for pooled and sex-specific jaguar density models

Table 3-B1. Key herbivore species (n = 7 species total) included in relative activity indices calculated per camera trap station for both parks (native prey only) and ranches (native prey plus domestic livestock) in the northern Brazilian Pantanal.

Common name	Scientific name	Average weight (kg)	Average group size (individuals)
Agouti	<i>Dasyprocta azarae</i>	3.00	1
Brazilian tapir	<i>Tapirus terrestris</i>	150.00	1
Collared peccary	<i>Pecari tajacu</i>	18.00	5
Domestic cattle	<i>Bos taurus</i>	175.00	10
Feral water buffalo	<i>Bubalus bubalis</i>	55.00	1
Red brocket deer	<i>Mazama americana</i>	20.00	1
White-lipped peccary	<i>Tayassu pecari</i>	28.00	75

Table 3-B2. Standardized  $\beta$  coefficient estimates ( $\pm$  SE) for jaguars in the park and ranch complex in the northern Brazilian Pantanal, wherein estimates include pooled density, sex-specific (h2) parameters for detection ( $g0$ ) and movement ( $\sigma$ ), sex-specific mixture parameter ( $pmix$ ), and model selection criteria ( $\Delta AICc$ ; AICc weight,  $w$ ) for the top 3 candidate and null models.

Model	<i>Density</i>				<i>g0</i>				<i>σ</i>		<i>pmix</i>
	Baseline	Cover	Wild RA <sub>ctI</sub>	Cattle RA <sub>ctI</sub>	Baseline	h2	Roads	h2 × Roads	Baseline	h2	h2
1	-8.25 (0.23)	0.79 (0.20)			-3.68 (0.22)	0.75 (0.27)	0.05 (0.33)	0.55 (0.38)	7.68 (0.11)	0.24 (0.13)	-0.27 (0.28)
2	-8.21 (0.23)	0.73 (0.21)		-0.41 (0.24)	-3.68 (0.22)	0.75 (0.27)	0.07 (0.33)	0.54 (0.38)	7.69 (0.11)	0.22 (0.13)	-0.24 (0.28)
3	-8.07 (0.19)		0.61 (0.24)		-3.67 (0.22)	0.78 (0.27)	-0.02 (0.32)	0.63 (0.38)	7.71 (0.12)	0.27 (0.14)	-0.33 (0.29)
Null	-7.93 (0.15)				-3.67 (0.22)	0.78 (0.27)	-0.04 (0.32)	0.62 (0.38)	7.69 (0.11)	0.27 (0.13)	-0.29 (0.28)

Table 3-B3. Top ( $\Delta\text{AICc} < 2.00$ ) and null male and female models for jaguars in the park and ranch complex in the northern Brazilian Pantanal, wherein reported models include covariates for density ( $D$ ), detection parameters ( $g0$ ;  $\sigma$ ), number of parameters ( $npar$ ), and model selection criteria ( $\Delta\text{AICc}$ ; AICc weight,  $w$ ).

Model	$npar$	$\Delta\text{AICc}$	$w$
<b>Female</b>			
$D\sim(\text{Wild prey } RA_{ctI}), g0\sim(\text{Roads}), \sigma\sim(1)$	5	0	0.18
$D\sim(\text{Cover}), g0\sim(\text{Roads}), \sigma\sim(1)$	5	0.38	0.15
$\text{Null}, D\sim(1), g0\sim(\text{Roads}), \sigma\sim(1)$	4	1.14	0.10
$D\sim(\text{Cattle } RA_{ctI}), g0\sim(\text{Roads}), \sigma\sim(1)$	5	1.25	0.10
$D\sim(\text{Cover} + \text{Cattle } RA_{ctI}), g0\sim(\text{Roads}), \sigma\sim(1)$	6	1.86	0.07
<b>Male</b>			
$D\sim(\text{Brocket deer } RA_{ctI}), g0\sim(\text{Roads}), \sigma\sim(1)$	5	0	0.11
$D\sim(\text{Brocket deer } RA_{ctI} + \text{Female jaguar density}), g0\sim(\text{Roads}), \sigma\sim(1)$	6	0.58	0.08
$\text{Null}, D\sim(1), g0\sim(\text{Roads}), \sigma\sim(1)$	4	0.72	0.08
$D\sim(\text{Cover}), g0\sim(\text{Roads}), \sigma\sim(1)$	5	0.83	0.07
$D\sim(\text{Female jaguar density}), g0\sim(\text{Roads}), \sigma\sim(1)$	5	0.88	0.07
$D\sim(\text{Brocket deer } RA_{ctI} + \text{Cover}), g0\sim(\text{Roads}), \sigma\sim(1)$	6	1.09	0.06
$D\sim(\text{Brocket deer } RA_{ctI} + \text{Cattle } RA_{ctI}), g0\sim(\text{Roads}), \sigma\sim(1)$	6	1.68	0.05

Table 3-B4. Standardized  $\beta$  coefficient estimates ( $\pm$  SE) and model selection criteria ( $\Delta$ AICc; AICc weight,  $w$ ) for the top 3 ranked best-fit ( $\Delta$ AICc < 2.00) and null male and female models for jaguars in the park and ranch complex in the northern Brazilian Pantanal.

Model	<i>Density</i>			<i>g0</i>		$\sigma$ (.)		
	Baseline	Cover	Wild prey RA <sub>ctI</sub>	Brocket deer RA <sub>ctI</sub>	Female density			
<b>Female</b>								
1	-8.70 (0.31)		0.79 (0.32)			-3.68 (0.22)	-0.01 (0.32)	7.72 (0.12)
2	-8.96 (0.40)	0.93 (0.29)				-3.68 (0.22)	0.07 (0.33)	7.69 (0.11)
3 ( <i>Null</i> )	-8.49 (0.22)					-3.67 (0.22)	-0.04 (0.32)	7.69 (0.11)
<b>Male</b>								
1	-8.81 (0.19)			-0.33 (0.22)		-2.91 (0.19)	0.59 (0.19)	7.96 (0.07)
2	-8.81 (0.18)			-0.31 (0.21)	0.27 (0.05)	-2.90 (0.15)	0.60 (0.19)	7.95 (0.07)
3 ( <i>Null</i> )	-8.78 (0.18)					-2.90 (0.15)	0.59 (0.19)	7.96 (0.07)

Table 3-B5. Predicted estimates ( $\pm$  SE) for annual sex-specific density ( $D$ ; individuals / 100 km<sup>2</sup>) and pooled detection parameters ( $g0$ ;  $\sigma$ , in meters) for the top 3 best-fit and model averaged models for male and female jaguars in the park and ranch complex in the northern Brazilian Pantanal.

Model	Density		$g0$		$\sigma$
	Ranch	Parks	On road	Off road	(.)
<b>Female</b>					
<i>D</i> ~(Wild prey $RA_{cl}$ ), <i>g0</i> ~(Roads), $\sigma$ ~(1)	2.98 (0.09)	2.44 (0.06)	0.02 (0.01)	0.02 (0.01)	2,253.90 (275.04)
<i>D</i> ~(Cover), <i>g0</i> ~(Roads), $\sigma$ ~(1)	2.36 (0.05)	1.91 (0.02)	0.03 (0.01)	0.02 (0.01)	2,181.93 (245.62)
Null, <i>D</i> ~(1), <i>g0</i> ~(Roads), $\sigma$ ~(1)	2.05 (< 0.01)	2.05 (< 0.01)	0.02 (0.01)	0.02 (0.02)	2,194.76 (245.31)
Model average	2.55 (0.06)	2.16 (0.03)	0.02 (0.01)	0.02 (0.01)	2,215.04 (257.84)
<b>Male</b>					
<i>D</i> ~(Brocket deer $RA_{cl}$ ), <i>g0</i> ~(Roads), $\sigma$ ~(1)	1.46 (< 0.01)	1.56 (< 0.01)	0.08 (0.01)	0.05 (0.01)	2,856.81 (205.39)
<i>D</i> ~(Brocket deer + Female jaguar density), <i>g0</i> ~(Roads), $\sigma$ ~(1)	1.66 (0.01)	1.60 (0.03)	0.09 (0.01)	0.05 (0.01)	2,883.62 (207.91)
Null, <i>D</i> ~(1), <i>g0</i> ~(Roads), $\sigma$ ~(1)	1.54 (< 0.01)	1.54 (< 0.01)	0.09 (0.01)	0.05 (0.01)	2,864.57 (210.04)
Model average	1.54 (0.01)	1.57 (0.01)	0.09 (0.01)	0.05 (0.01)	2,867.23 (207.48)

Table 3-B6. Moran's index ( $I$ , z-score in parentheses; all  $p$ -values < 0.05) for annual density surfaces predicted from the selected best-fit male and female jaguar models in the park and ranch complex in the Brazilian Pantanal.

Model	Ranch			Park		
	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
<b>Female</b>						
<i>D~(Wild prey RA<sub>ci</sub>I), g0~(Roads), σ~(1)</i>	0.52 (83.32)	0.37 (58.29)	0.91 (115.27)	0.73 (74.22)	0.70 (71.47)	0.50 (54.01)
<i>D~(Cover), g0~(Roads), σ~(1)</i>	0.52 (82.58)	0.50 (78.36)	0.55 (69.62)	0.71 (72.13)	0.71 (72.13)	0.71 (72.13)
<i>Null, D~(1), g0~(Roads), σ~(1)</i>	1.00 (158.55)	1.00 (157.37)	1.00 (126.38)	1.00 (101.56)	1.00 (101.56)	1.00 (101.56)
<i>Model average</i>	0.52 (83.21)	0.38 (59.87)	0.64 (80.53)	0.71 (72.18)	0.65 (66.00)	0.53 (56.27)
<b>Male</b>						
<i>D~(Brocket deer RA<sub>ci</sub>I), g0~(Roads), σ~(1)</i>	0.62 (98.40)	0.80 (125.40)	0.77 (97.66)	0.68 (68.72)	0.68 (69.52)	0.61 (61.52)
<i>D~(Brocket deer + Female jaguar density), g0~(Roads), σ~(1)</i>	0.52 (83.31)	0.39 (62.12)	0.78 (98.58)	0.59 (59.91)	0.71 (71.79)	0.46 (48.69)
<i>Null, D~(1), g0~(Roads), σ~(1)</i>	1.00 (158.55)	1.00 (157.37)	1.00 (126.38)	1.00 (101.56)	1.00 (101.56)	1.00 (101.56)
<i>Model average</i>	0.63 (99.78)	0.50 (77.97)	0.80 (101.57)	0.64 (65.03)	0.70 (71.63)	0.48 (50.42)

Appendix 3-C. Input file structure and example code for analyses in R package ‘secr’ (Efford 2016)

File 3-C1. Example capture history input for R package ‘secr’ (CH.txt).

```
#Session ID Occasion trapID Sex Year Site
2011 2 4 F08 F 2011 Ranch
2011 2 1 F20 F 2011 Ranch
2011 3 1 F11 F 2011 Ranch
###
```

File 3-C2. Example camera trap survey array (traps) input for R package ‘secr’, including coordinates (UTM), operational days (‘Usage’) and site level covariates (On or Off road; distance from water; cover type; traps.txt).

```
# Session trapID X Y Usage /Road Water_Dist Covtype
F01 524658 8081383 111111 /On 501.17 Forest
F02 525661 8085226 111111 /On 742.21 Forest
F03 529540 8087460 111111 /Off 44.17 Forest
###
```

File 3-C3. Example habitat mask (state-space) input file for R package ‘secr’, with coordinates (UTM), site, and covariates extracted per pixel (mask.txt).

```
X Y Site River_index Cover Domestic_index Wild_index Session
526723.379 8046447.079 Ranch 0 0.240 19815.071 5404.246 year1
527408.029 8046447.079 Ranch 0 0.120 32386.442 4673.636 year1
528092.679 8046447.079 Ranch 0 0.170 36302.283 5419.061 year1
###
```



File 3-C4. Example code for running a model in R package 'secr'.

```
#####  
#EXAMPLE 'secr' CODE: JAGUARS  
#####  
setwd('/jaguars')  
getwd()  
  
library(secr)  
library(secrdesign)  
library(maptools)  
library(sp)  
library(rgdal)  
library(ggplot2) #For fancier plots  
library(maps)  
  
#Read capture histories (CH) and camera trap array (traps)  
jagCHranch1 <- read.caphist(captfile = 'ranchyear1_CH.txt', 'ranchyear1_traps.txt', detector =  
'proximity', covnames = c('Sex', 'Year', 'Site'), trapcovnames = c('Roads', 'Water_Dist', 'Covtype'))  
head(jagCHranch1) #check data were successfully read in  
  
jagCHranch2 <- read.caphist(captfile = 'ranchyear2_CH.txt', 'ranchyear2_traps.txt', detector =  
'proximity', covnames = c('Sex', 'Year', 'Site'), trapcovnames = c('Roads', 'Water_Dist', 'Covtype'))  
  
jagCHranch3 <- read.caphist(captfile = 'ranchyear3_CH.txt', 'ranchyear3_traps.txt', detector =  
'proximity', covnames = c('Sex', 'Year', 'Site'), trapcovnames = c('Roads', 'Water_Dist', 'Covtype'))  
  
jagCHpark1 <- read.caphist(captfile = 'parkyear1_CH.txt', 'parkyear1_traps.txt', detector = 'proximity',  
covnames = c('Sex', 'Year', 'Site'), trapcovnames = c('Roads', 'Water_Dist', 'Covtype'))  
  
jagCHpark2 <- read.caphist(captfile = 'parkyear2_CH.txt', 'parkyear2_traps.txt', detector = 'proximity',  
covnames = c('Sex', 'Year', 'Site'), trapcovnames = c('Roads', 'Water_Dist', 'Covtype'))
```

```

jagCHpark3 <- read.caphist(captfile = 'parkyear3_CH.txt', 'parkyear3_traps.txt', detector = 'proximity',
covnames = c('Sex', 'Year', 'Site'), trapcovnames = c('Roads', 'Water_Dist', 'Covtype'))

#create main capture history for pooled models
jagCHpr123 <- MS.caphist(jagCHranch1, jagCHranch2, jagCHranch3, jagCHpark1, jagCHpark2,
jagCHpark3)
head(covariates(jagCHpr123))
verify(jagCHpr123) #check for any errors

# Fix different CH lengths via
<http://www.phidot.org/forum/viewtopic.php?f=36&t=3138&p=10136&hilit=levels+of+fix+covariate#p10136>
for (i in 1:length(jagCHpr123))
  covariates(jagCHpr123[[i]])$Site <- factor(covariates(jagCHpr123[[i]])$Site,
      levels = c('Ranch', 'Park'))
lapply(covariates(jagCHpr123), function(x) levels(x$Site))
verify(jagCHpr123) #verify correct now...
summary(jagCHpr123, terse = T) #get summary of pooled capture histories

#Set traps objects for each survey site and year
trapsranch1 <- read.traps('ranchyear1_traps.txt', detector = 'proximity', covnames = c('Roads',
'Water_Dist', 'Covtype'))

trapsranch2 <- read.traps('ranchyear2_traps.txt', detector = 'proximity', covnames = c('Roads',
'Water_Dist', 'Covtype'))

trapsranch3 <- read.traps('ranchyear3_traps.txt', detector = 'proximity', covnames = c('Roads',
'Water_Dist', 'Covtype'))

trapspark1 <- read.traps('parkyear1_traps.txt', detector = 'proximity', covnames = c('Roads', 'Water_Dist',
'Covtype'))

trapspark2 <- read.traps('parkyear2_traps.txt', detector = 'proximity', covnames = c('Roads', 'Water_Dist',
'Covtype'))

```

```
trapspark3 <- read.traps('parkyear3_traps.txt', detector = 'proximity', covnames = c('Roads', 'Water_Dist',  
'Covtype'))
```

```
#Develop the mask with centered and standardized covariates ("..._std") for all survey sites and years...
```

```
# Masks developed from satellite imagery;
```

```
# predicted prey biomass index layers processed in ArcGIS; and
```

```
# all values extracted to user-defined mask pixels = 700m spacing
```

```
maskranch1 <- read.mask(file = 'mask_ranchyear1.txt', spacing = 700, header = TRUE, columns =  
c('Site', 'River_index_std', 'Cover_std', 'Domestic_index_std', 'Wild_index_std', 'Session'))
```

```
maskranch2 <- read.mask(file = 'mask_ranchyear2.txt', spacing = 700, header = TRUE, columns =  
c('Site', 'River_index_std', 'Cover_std', 'Domestic_index_std', 'Wild_index_std', 'Session'))
```

```
maskranch3 <- read.mask(file = 'mask_ranchyear3.txt', spacing = 700, header = TRUE, columns =  
c('Site', 'River_index_std', 'Cover_std', 'Domestic_index_std', 'Wild_index_std', 'Session'))
```

```
maskpark1 <- read.mask(file = 'mask_parkyear1.txt', spacing = 700, header = TRUE, columns = c('Site',  
'River_index_std', 'Cover_std', 'Domestic_index_std', 'Wild_index_std', 'Session'))
```

```
maskpark2 <- read.mask(file = 'mask_parkyear2.txt', spacing = 700, header = TRUE, columns = c('Site',  
'River_index_std', 'Cover_std', 'Domestic_index_std', 'Wild_index_std', 'Session'))
```

```
maskpark3 <- read.mask(file = 'mask_parkyear3.txt', spacing = 700, header = TRUE, columns = c('Site',  
'River_index_std', 'Cover_std', 'Domestic_index_std', 'Wild_index_std', 'Session'))
```

```
####
```

```
#MODELS with centered and standardized covariates ("..._std")
```

```
####
```

```
#Example model: read in full capture histories, list of associated masks,
```

```
# set Conditional Likelihood (CL) = FALSE (to allow for covariates on Density, D~), and...
```

```
# include mixture model (hcov = 'Sex') argument to allow sex-specific parameter on...
```

```
# detection ( $g_0$ ,  $\sigma \sim h_2$ ), which also provides output for parameter 'pmix' ...
```

```

# Start = initial parameter values for D, g0, sigma determined via function in 'secr' based on CH;
# see 'secr' Parameterisations vignette.

#Example model (D ~ COVER + CATTLE, g0 ~ h2 * ROADS, sigma ~ h2)
jags_examplemodel <- secr.fit(jagCHpr123, mask = list(maskranch1, maskranch2, maskranch3,
maskpark1, maskpark2, maskpark3), CL = FALSE, hcov = 'Sex', start = list(D = 0.0007, g0 = 0.085,
sigma = 1265), model = list(D ~ (Cover_std + Domestic_index_std), g0 ~ (h2 * Roads), sigma ~ h2))

#Save output as .rds (model, coefficients) and write .csv
saveRDS(jags_examplemodel, 'jags_examplemodel.rds')
coef_jags_examplemodel.rds <- print(coef(jags_examplemodel.rds))
write.csv(coef_jags_examplemodel.rds, 'coef_jags_examplemodel.csv')

#Generate predictions: read in .rds, develop newdata argument for parameters;
# here, (Cover = 0, since is standardized will represent average value of canopy cover); then
# produce predictions for Density, g0, and sigma...
jags_examplemodel.rds <- readRDS('jags_examplemodel.rds')

jags_newdata1 <- data.frame(Cover_std = rep(0,2), cat1_std = rep(0,2), h2 = c('M', 'F'), Roads = c('On',
'Off'))
jags_newdata2 <- data.frame(Cover_std = rep(0,2), cat1_std= rep(0,2), h2 = c('M', 'F'), Roads = c('Off',
'On'))

jags_examplemodel_prediction1 <- predict(jags_examplemodel.rds, newdata = jags_newdata1)
write.csv(jags_examplemodel_prediction1, file = 'jags_examplemodel_prediction1.csv')

jags_examplemodel_prediction2 <- predict(jags_examplemodel.rds, newdata = jags_newdata2)
write.csv(jags_examplemodel_prediction2, file = 'jags_examplemodel_prediction2.csv')

#Now predict density surface (Dsurface) to mask and export as .csv for further analysis in ArcGIS
surface_jags_examplemodel <- predictDsurface(jags_examplemodel.rds)
options(max.print=10000) #reset max print to show all rows of data here and in export (default = ~3600
rows)

```

```
#Print density surface (Dsurface) estimate per mask pixel, then export to .csv
print(surface_jags_examplemodel)
printsurface_jags_examplemodel <- capture.output (print(surface_jags_examplemodel))
saveRDS(printsurface_jags_examplemodel, 'printsurface_jags_examplemodel.rds') #
printsurface_jags_examplemodel.rds <- readRDS(' printsurface_jags_examplemodel.rds')

#SAVE printed Dsurface as .csv for further processing and eventual read-in to ArcGIS...
write.csv(printsurface_jags_examplemodel.rds, 'printsurface_jags_examplemodel.csv')

###END###
```

**CHAPTER 4: RESOURCE SELECTION AND DENSITY-DEPENDENT DRIVERS OF  
JAGUAR (*PANTHERA ONCA*) MOVEMENT IN THE  
BRAZILIAN PANTANAL**

**ABSTRACT**

Animals exhibit density-dependent responses in population vital rates (e.g., survival) and behavior, yet responses in resource selection remain little explored. Resource selection by animals is sensitive to landscape context, and as such, variations in conspecific density may alter expectations of animal space use and, by extension, their responses to land management. Throughout the Brazilian Pantanal jaguar and their prey are dependent upon forest cover and become concentrated in remnant forest patches in working landscapes, which elevates local jaguar densities compared to intact forest regions. In resource selection functions at the scale of jaguar home ranges ( $n = 14$  individuals total), daily foraging bouts ( $n = 2,638$  foraging bouts total), and individual steps ( $n = 400$  steps total), jaguar density interacted with wild prey activity, cattle activity, and forest cover to determine selection patterns ( $\Delta AIC$  alternatives  $> 2.00$ ). I expected that jaguars would not necessarily avoid high density areas, but instead change selection of other (i.e., food; security cover) resources in areas with high versus low conspecific densities. When density was not considered, I observed greater model selection uncertainty and loss of precision on parameter estimates at the foraging scale. Male jaguars were more vagile than females and likely encountered greater variation in conspecific density, but female jaguars responded more strongly to density in their resource selection. At the population level, generalist species like jaguars will distribute to areas with higher wild prey activity and canopy cover. Individual jaguars may, however, respond differently to conspecific density, cattle, and proximity to anthropogenic features like roads, based on age class or life history stage (e.g., individual at age of dispersal seeking to establish territory and thus ‘pushed’ to more open habitat versus dominant resident individual with territory in high resource areas; female with young cubs concentrating movement and activity in core home range, versus female without

cubs using entire home range). As habitat becomes increasingly fragmented and jaguars aggregate in remaining resource patches, individuals may leave ‘safe’ habitat and, driven by conflict with conspecifics, move into riskier (i.e., areas with less forest cover and greater odds of encountering humans and cattle) landscapes.

**KEY WORDS:** density-dependence; habitat selection; *Panthera onca*; predator; prey; relative activity index; resource selection function; step selection function; telemetry

## INTRODUCTION

Density-dependent responses are generally considered important in applied wildlife conservation when a sensitive population vital rate is involved, such as survival or recruitment (Guthery and Shaw 2013). At one extreme, where density has been driven low, Allee effects may further drive a population toward extinction given increasing difficulty in securing mates (Courchamp et al. 1999). For example, when pack sizes of social canids like African wild dogs (*Lycaon pictus*) become too small, recruitment declines as the number of adults is not sufficient to successfully defend vulnerable pups (Courchamp et al. 1999). At the other extreme, high density populations suffer reduced rates of survival or recruitment due to inter-specific competition for resources (Bonenfant et al. 2009). Density-dependent changes in behavior between these extremes has been observed in several taxa (Fowler 1987, Fuller et al. 2007, Bonenfant et al. 2009), and is generally considered of less immediate conservation concern. The focus on vital rates implies a large-scale, population-level response to changes in overall density. Yet, spatial variation within a population exposes individuals to patchiness in resources and risks, including variation in conspecific density. Thus, an individual animal must negotiate risks and rewards within the context of density variation in their routine movements (Kjellander et al. 2004, Vander Wal et al. 2014).

In landscapes modified by human activities, where the distribution of resources and risks may change rapidly and core patches of habitat may be increasingly small and fragmented, changes in resource selection due to local levels of conspecific density likely foreshadows the larger-scale, population-level

reductions in overall population condition (Guthery and Shaw 2013). Indeed, prior research has demonstrated direct impacts of density dependence on habitat selection in voles (*Microtus pennsylvanicus*; Morris and MacEachern 2010) and on the mating systems of several species including red deer (*Cervus elaphus*; Clutton-Brock et al. 1997, Kokko and Rankin 2006). Thus, as a precautionary measure, greater understanding of density-dependent responses in the routine movements of animals is needed to enable rapid and effective conservation at the population level (Mitchell and Hebblewhite 2012).

The proliferation of GPS-based tracking of animals has enabled observations of habitat use by animals at ever-finer spatial scales (Lele et al. 2013), although this spatially- and temporally-dynamic information is often related to a static distribution of resources which limits inference on the mechanisms driving animal behavior (Hebblewhite and Haydon 2010). Tracking the movement of individuals in response to local conspecific density is needed to gain greater inference into endogenous population processes that might drive observed differences in resource selection across populations, especially in heterogeneous landscapes (Wiens 1997, Cagnacci et al. 2010, Thurfjell et al. 2014). Pairing fine-scale movement data with spatially-explicit estimates of conspecific density, and spatio-temporally varying availabilities of prey, may provide a window of opportunity for exploring density-dependent resource selection decisions. In prior studies, such pairings have included resource selection patterns as a variable driving local animal density via a static prediction map. Taking resource selection into account had the advantage of accounting for heterogeneity in space (habitat) use, leading to increased precision in parameter estimation of density and detection (Royle et al. 2013, Proffitt et al. 2015, Boyce et al. 2016). Yet local resource levels, not resource selection behavior, ultimately set constraints on density. As such, covariates on resources alone have been predictive of local animal density (Chapter 3). Density, in turn, is a spatio-temporally integrated population-level measure that sets a local context in response to how resource selection behavior might vary among individuals.

In order to estimate resource use of a given species, resource selection functions (RSFs) are statistically rigorous models which provide values proportional to the probability of use (Boyce et al.



2002). Conditional multi-scale RSFs (Manly et al. 2002) paired used and randomly generated available points across the landscape to account for potentially limiting resources in an animal's home range, daily movement, or hourly movement (Leblond et al. 2011). Step selection functions (SSFs) provide a valuable tool for quantifying movement (Thurfjell et al. 2014, Avgar et al. 2016, Signer et al. 2019) as well as the drivers of individual decision-making behavior by matching observed steps (straight line displacement between consecutive points) to landscape and resource covariates.

RSF and SSF analyses provide inference on overall (population-level) and specific (individual-level) use, respectively, commonly envisioned on different levels of organization such as selection of geographic range (first order), selection of home range within the geographic range (second order), seasonal use within the home range (third order), and individual foraging choices (fourth order; Johnson 1979). For example, species may show predator avoidance at large spatial scales but overlap at finer spatial scales, thereby demonstrating that species responses to a given landscape feature may indeed be scale-dependent (Basille et al. 2015). Animal densities are expected to vary to balance individual fitness (Fretwell and Lucas 1970, Beckmann and Berger 2003), with lower quality habitats requiring larger individual animal movements to secure resources. Individuals may even further subdivide space use (e.g., diel cycle) to avoid competition or antagonistic interactions with conspecifics or interspecific competitors (Pimm et al. 1985). As such, conspecific density is expected to interact with local resource levels to drive resource selection patterns.

Large, solitary carnivores like jaguars (*Panthera onca*; Quigley et al. 2017) and tigers (*Panthera tigris*) maintain large, presumably exclusive territories to secure food and mates (Carter et al. 2015). Such patterns of space use have direct implications for conservation and management decisions, especially in multi-use, working landscapes like cattle ranches where native prey may be increasingly concentrated in remnant habitat patches (Desbiez et al. 2009, Schmidt and Kuijper 2015), and livestock might artificially inflate carnivore densities potentially increasing antagonistic interactions and competition among conspecifics (Quigley et al. 2015). Herein, I examined the role of scale- and density-dependent resource selection by jaguars in a complex of working cattle ranches and protected areas in the Brazilian Pantanal.

The ranches followed “wildlife friendly” practices designed to enhance human-tolerance for jaguars (e.g., via ecotourism to offset losses of livestock) and increase the conservation value of the multiple-use landscapes that dominate jaguar range (of which 5% of the Pantanal is protected, 95% privately owned, and 80% used to ranch livestock; Quigley and Crawshaw 1992, Seidl et al. 2001, Tomas et al. 2019). Hunting of jaguars and prey was prohibited, with evidence mounting that provisioning of livestock may artificially elevate local jaguar densities (Chapter 3) and increase the risk of infanticide (Tortato et al. 2017). Greater understanding of the drivers of jaguar space use in such working landscapes is necessary to help mitigate jaguar-human conflict while meeting conservation goals for jaguars.

## METHODS

### *Study Area*

This study was conducted in a working cattle ranch and protected area complex in the northern Brazilian Pantanal (Fig. 4-1; Alho et al. 1988). Encompassing an area of about 140,000 km<sup>2</sup>, this seasonally inundated floodplain includes a mosaic of riparian, semi-deciduous, and dry forest (*cerrado*) habitat (Prance and Schaller 1982, Fortney et al. 2004). The Pantanal is characterized by wet and dry seasons (November – April; May – October, respectively), and nearly two-thirds of the annual 1,300 mm precipitation falls during the wet season (Zeilhofer and Schessl 1999). Nearly 95% of the Pantanal is privately owned and over 80% dedicated to large-scale, high-intensity cattle ranches (Quigley and Crawshaw 1992, Seidl et al. 2001).

### *Resource and Conspecific Covariates*

Resources in this study included habitat (e.g., forest cover; river distance) and prey covariates. Roads were mapped using a GPS unit (Garmin eTrex Legend HCx), and rivers and percent forest cover were mapped from national layers provided by collaborators (ICMBio\CENAP 2010). Key prey for jaguars in these landscapes were agouti (*Dasyprocta azarae*), brocket deer (*Mazama* spp.), collared peccary (*Pecari tajacu*), white-lipped peccary (*Tayassu pecari*), tapir (*Tapirus terrestris*), and cattle (*Bos*

*taurus*; Chapters 2, 3). To capture variation in prey availability for jaguars, I predicted the relative activity of each individual species from previous modeling efforts (Chapter 2) and summed values across species to yield a composite wild prey activity index. Conspecific density surfaces were estimated from spatially-explicit capture-recapture (SCR) models, with models fitted for overall jaguar density as well as separately for male and female jaguar (Chapter 3). These models indicated that jaguar density largely reflected percent forest cover across both the protected parks and the working ranches. All covariates were predicted to the study area using map algebra in ArcMap (v.10.3, ESRI 2018) or SCR analyses in program R package ‘secr’ (Efford 2016). I produced rasters in ArcGIS with a predefined cell size of 0.49km<sup>2</sup>, selected by prior analyses where I adjusted grain size from 0.10 to 5.00km<sup>2</sup> (Chapter 3) to determine the optimal scale for model fitting and parameter estimation. No covariates were highly correlated (Pearson correlation  $r < 0.70$ ; Fig. 4-A2) and all were therefore standardized and included in candidate models as described below.

### *Satellite telemetry*

A total of 14 jaguars were fitted with GPS collars (Globalstar, Vectronic Aerospace, Germany) and tracked between 2011–2014 (Fig. 4-2; Table 4-B1; Morato et al. 2018a). Jaguars were captured using soft-hold footsnare (Frank et al. 2003) and immobilized by a government-certified wildlife veterinarian using a Telazol and Zolazepam mixture (Zoletil, Virbac do Brasil). All procedures were approved by permitting government agencies and university committees (see Ethical Statement). Collars operated 24 hours per day and were programmed to record locations every 4 hours for a total of 6 fixes per day. Collar fix rate success ranged from 60% (under 100% canopy cover) to 95% (in open areas) and had an observed lifespan of anywhere from 3 months to 1.5 years (average lifespan = 6 months; Hofman et al. 2019). Each collar was fitted with a programmed drop-off unit (Vectronic Aerospace, Germany), with the collar automatically released after 104 weeks (recovery success = 3 collars recovered; all collars dropped off as programmed). I estimated dry season home range size of all telemetered individuals using minimum convex polygons (Table 4-B1; biometric data, Table 4-B2). Data were retained and RSF and iSSF models

fit during the dry season only, coinciding with the period during which camera trap surveys were conducted to provide information on prey activity (Chapter 2) and jaguar density (Chapter 3).

#### *Population-Level Resource Selection Functions (RSFs)*

I tested population-level conditional use to availability within seasonal ranges (third order), and along daily and step length movement paths (fourth order) using logistic regression in program R packages ‘lme4’ (Bates et al. 2015) and ‘survival’ (Therneau 2015). Determining the appropriate spatial scale is key with RSFs, and including covariates at multiple grains (spatial resolutions) improves estimates and model predictions, by accounting for potential differences in species’ responses to resources at multiple spatial scales (Meyer and Thuiller 2006). Therefore, due to uncertainty regarding the appropriate scale at which to observe path-level selection decisions, I explored availability at multiple grains, from 500 m (average distance between two consecutive points, or average step length) to 5 km (average daily movement rate) scales. I generated random (available) points at the home range level (Table 4-B1) for each telemetered individual using a sampling intensity of 0.01 locations per km<sup>2</sup>. Using the Geospatial Modelling Environment (GME v.0.7.4.0; Beyer 2015), I then generated random points conditional on each used location along each animals’ movement path at two different spatial scales, with 5 random (available) points selected within a 5-km buffer (the scale of average daily movement rate) and another 5 random points selected within a 500-m buffer (the scale of average 4-hr displacements). Covariates were extracted for each used and available point.

I used conditional logistic regression to quantify habitat conditions associated with observed versus available points across the landscape (Fortin et al. 2005), with resource selection ( $w(x)$ ) estimated in log-linear form with coefficient  $\beta_n$  for covariate  $x_n$  as

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \quad (1)$$

The full RSF model was defined as

$$w(x) = \exp(\text{cover} + \text{road distance} + \text{river distance} + \text{wild prey activity} + \text{cattle activity} + \text{jaguar density} + (\text{jaguar density} \times \text{cover}) + (\text{jaguar density} \times \text{wild prey}) + (\text{jaguar density} \times \text{cattle}) + (\text{jaguar density} \times \text{river}) + (1 \mid \text{jaguar ID})) \quad (2)$$

I also tested brocket deer activity alone as an alternative to wild prey activity, as this was an important covariate in prior analyses (Chapters 2, 3), yet it was not among the top competing models and so is not reported herein.

For all continuous covariates, nonlinear fits were tested by inclusion of second order polynomial terms. I compared this full model, which included effects for jaguar density and interactions between jaguar density and responses to other landscape covariates to two sets of simplified models that included jaguar density without interaction terms, or without jaguar density all together. I compared models using Akaike's Information Criterion ( $\Delta\text{AIC} < 2.00$ ) and AIC weight ( $w_i$ , Burnham and Anderson 2002). I then extracted the most parsimonious model using backwards AIC-based model selection, requiring the inclusion of any main effect, polynomial term, or interaction to contribute at least 2 units of AIC to be retained in the final model (Arnold 2010). I considered changes in the sign and magnitude of the conditional and marginal estimates for the jaguar density coefficient to ascertain the need to account for individual variation (Gillies et al. 2006).

#### *Individual-Level Integrated Step Selection Functions (iSSFs)*

I evaluated the degree of variation in individual behavioral responses (i.e., movement rate; directionality) to conspecific density. Within the ranching landscape only, iSSFs (Forester et al. 2009) were fit to a subset of 6 jaguars (3 males, 3 females with sufficient GPS data over at least 2 consecutive months of dry season data.) using a maximum likelihood framework in program R (R Core Team 2018) package 'amt' (Signer et al. 2019; see code in Appendix 4-E). One step was defined as the straight-line distance between consecutive (4-h interval) GPS points. Each observed step was paired with 5 random

(available) steps (Fortin et al. 2005, Avgar et al. 2016); I used a gamma distribution for step length and von Mises distribution for turn angle (Signer et al. 2019).

For the step selection function, I included step length and turn angle as covariates (see Eq. 3) to minimize selection bias (Forester et al. 2009), along with covariates hypothesized to influence individual movement (Potts et al. 2014) which included landscape structure (percent canopy cover), spatio-temporal food resource activity (wild and domestic prey activity), and conspecific density (when Pearson correlation  $r < 0.70$ ). Importantly, for this analysis density estimates were refit excluding the target animal. The full model for the influence of environmental, food resource, or conspecific densities on an individual jaguar's directional persistence included the given covariate (i.e., canopy) and parameters for step strata (step\_id\_), log of step length (log\_sl), and cosine of turn angle (cos\_ta) to develop a full model as

$$\begin{aligned} i\text{SSF} = & (\text{jaguar density} + \text{jaguar density:cos\_ta} + \text{jaguar density:log\_sl} + \\ & \text{log\_sl} * \text{cos\_ta} + \text{strata}(\text{step\_id\_})) \end{aligned} \quad (3)$$

To control for autocorrelation for each collared individual  $i$ , steps were paired with conspecific density surfaces calculated after removal of individual  $i$  from the capture histories (i.e.,  $n-i$  capture histories used to develop a density surface for  $n$  population minus individual  $i$ ). Best-fit models were selected using Akaike's Information Criterion corrected for small sample sizes (AICc) and AICc weight ( $w_i$ , Burnham and Anderson 2002).

## RESULTS

On average, jaguar dry season home ranges in the park and ranch study areas covered 77.05 ( $\pm$  13.82 SE) km<sup>2</sup>. Males had an average home range size of 108.45 ( $\pm$  16.64 SE) km<sup>2</sup> and daily movement rate (average 24-h displacement) of 4.89 km, while females ranged over territories of 35.19 ( $\pm$  5.28 SE) km<sup>2</sup> and moved on average 3.90 km per day (Table 4-B1). Jaguars responded to each covariate on different spatial grains, with best-fit models including wild prey activity (per pixel), cover (500 m grain), and 5 km grain size for the remaining covariates (jaguar density; cattle activity). Within dry season home

range, there was strong evidence that adult jaguars selected for areas of higher jaguar density and, in those high density areas, a positive relationship between jaguar density, increased canopy cover, and high cattle activity with a negative relationship between conspecific density and distance from river ( $\Delta AIC$  alternatives  $> 2.00$ ; Tables 4-2, 4-3; Fig. 4-3). For foraging along each step length (500 m buffer; Table 4-4), the best-fit model included a positive relationship between high jaguar density and cover, and negative relationships between high jaguar density, high cattle activity, and distance from river (Table 4-4; Fig. 4-4). There were differences in coefficient sign and significance between the top models with jaguar density and without jaguar density, resulting in differences in interpretation (Gillies et al. 2006).

For each individual jaguar included in the iSSF analyses, I fit conspecific density as a covariate for both turn angle and step length (Tables 4-B3, 4-B4; Appendices 4-C, 4-D), and fit diurnal and nocturnal time intervals to evaluate the degree to which time of day had an effect on directionality and distance moved (Appendix 4-C). Female jaguars exhibited greater sinuosity and step length during the night compared to the day, while males had greater directional persistence in both day and night and travelled over longer distances (Fig. 4-C1). Each female tended to travel longer distances at night in areas with high conspecific densities, and maintained directional persistence in those areas (Figs. 4-C2-4). Each male demonstrated greater diurnal directional persistence in areas with low conspecific density, and greater sinuosity in areas with high conspecific density, especially at night, indicating searching (hunting) behavior (Figs. 4-C5-7).

## DISCUSSION

The response of jaguars to wild prey activity at the finest scale (per pixel), and on a relatively fine spatial scale to security cover likely reflects the opportunistic, ambush predation methods used by jaguars, and the need to search an area to maximize encounter rate with prey (Bell 1991, Benhamou 1992). As jaguars are generalist predators that, rangewide, consume over 80 different species (Foster et al. 2010), the interaction with prey and canopy cover is especially important in working landscapes such as in this cattle ranch complex. In this study, the population level response was consistently negatively related to

cattle – which was expected, as ranch cowboys actively managed the herds and used anti-predation techniques including night corrals and defensive breeds like Pantaneiro bulls (Quigley et al. 2015).

The strong relationship between jaguars and habitat selection at two different spatial scales is novel because it captures not only the response of predators to prey and security cover, but also scale-dependent response to other jaguars. Interestingly, response to conspecifics was best-fit at the daily movement grain (average at 5 km grain size) – indicating that this likely tracks with territorial (daily) movement over a broader scale (e.g., scent marking along trails by male jaguars; Harmsen et al. 2010). As evidenced herein, within dry season ranges, jaguars tended to concentrate use in areas with relatively higher conspecific densities (average density at peak predicted use = 4.67 individuals / 100 km<sup>2</sup>, versus lowest predicted use = 0.50 individuals / 100 km<sup>2</sup>). This was likely due to provisioning of large-bodied livestock, where multiple resident jaguars were previously recorded visiting the same cow carcass in a single night and even cases of infanticide (Tortato et al. 2017). Additionally, several telemetered individuals were established residents of the study area, and multiple dominant jaguars were previously observed aggregating at a single cattle carcass (Tortato et al. 2017) and, sometimes, exhibited social tolerance behaviors as seen in pumas (*Puma concolor*; Elbroch et al. 2017). Due to the wildlife-friendly practices of (and sustained native prey populations within) the ranch complex (Quigley et al. 2015), this population of jaguars may be more tolerant of conspecifics than other local populations (Kanda et al. 2019) yet individuals will still exhibit conspecific aggression at cattle carcasses. Such responses make sense as jaguars are highly mobile, with distributions driven not only by prevailing (static) landscape conditions but also by the dynamic flooding regime (Crawshaw and Quigley 1991), movement (availability) of prey, and territoriality of conspecifics. Density dependence been previously demonstrated in other species including martens (*Martes americana*; Fryxell et al. 1999), whereby populations had density-dependent growth rates due to variation in both conspecific abundance and prey density.

Individual movement behaviors examined using iSSFs indicated that certain females tended to move more quickly through areas of higher conspecific density, as evidenced by greater directional persistence and longer displacement. This is likely a means of reducing time spent in those areas with



high conspecific density, and therefore of potentially avoid interspecific encounters (Morato et al. 2018b). Several individual jaguars had territories in the central region of the study site (Table 4-2; Fig. 4-A1) and along riverbanks – areas with high conspecific density (4-6 individuals / 100km<sup>2</sup>; Chapter 3, Soisalo and Cavalcanti 2006). As the study was conducted during the peak dry season, the river may serve as a linear feature useful for marking territories and as a prime location for hunting more aquatic prey like capybara and caiman. Individual jaguars exhibited increased sinuosity near to rivers, presumably to increase encounter rate with prey (Holling 1959, Bell 1991, Benhamou 1992). Thus, jaguars may tend to aggregate along linear features including waterways at the risk of encountering conspecifics, offset by the benefit of hunting relatively abundant aquatic and semi-aquatic prey during the dry season.

A recent study found that both male and female jaguars moved to maximize the probability of encountering other monitored females, while females tended to avoid areas where males remained (Kanda et al. 2019). The risk increases when females bring vulnerable cubs at age of weaning to cattle carcasses, where cubs encounter unrelated, aggressive competitors and can result in injury or death of cub or adult female. Such a response was previously observed in the southern Pantanal, where a female jaguar with cubs encountered a female puma with a single cub; in this instance, the female jaguar killed the adult puma (Crawshaw and Quigley 1984). Within the present ranch complex, we previously recorded two cases of infanticide (Tortato et al. 2017), both of which were likely a result of the aggregation of jaguars on cattle carcasses. As jaguars selected for high cover when in areas with high conspecific density, this may indicate possible density-dependent avoidance to mitigate the threat of antagonistic interactions.

In camera trap surveys, males were more detectable along linear features including roads, likely because linear features facilitate territorial marking in the form of scrapes and spray (Chapter 3; Harmsen et al. 2010, Sollmann et al. 2011). Conversely, females tended to avoid roads presumably to reduce chance of encounter with competing jaguars, especially territorial males, while accompanied by vulnerable cubs. While males were indeed more risk-tolerant than females (Conde et al. 2010), males may still mitigate the risk of encountering humans when travelling in open canopy (pasture) habitat by moving longer distances at night, and by still being active yet moving shorter distances during the day. Similar

patterns were found in cheetahs (*Acinonyx jubatus*), where telemetered individuals moved longer straight-line distances in areas with high cattle abundance (Broekhuis et al. 2019).

As with most large carnivore movement studies, an important consideration is that this dataset was limited by a small sample size, including the persistent issue of limited collar functionality (Hofman et al. 2019). Collar lifespan was significantly shorter than anticipated (expected 2 year minimum), as most collars functioned anywhere from 3 months to 1.5 years. The collars were likely compromised due to the highly aquatic nature of jaguars, where a single female was recorded swimming a 300m wide river 5 times over 7 days. Jaguars in this study region also swim with the river current to travel and hunt caiman (*Caiman yacare*) and capybara (*Hydrochaeris hydrochaeris*), often diving under water while in pursuit. Thus, the GPS and battery units were exposed to high levels of water stress compared to telemetered felids that occur in more arid environments (e.g., cheetah; puma; snow leopard, *Panthera uncia*) and had significantly greater success in fix rate and collar lifespan in other study areas (Hofman et al. 2019). Future studies on jaguars in naturally inundated landscapes should carefully consider GPS unit housing and collar durability, with sufficient testing to ensure satisfactory water resistance before deployment. Still, this present study reveals a useful line of inquiry into how different individuals and different sexes may perceive the relative risks and composition of a local landscape.

As habitat is increasingly fragmented to meet growing demands of global meat production and agriculture, native species are left to organize in smaller patches of remaining security cover and food resources (Desbiez et al. 2009). The introduction of conspecific density to resource selection represents a synthesis of concepts, supported by multi-scale RSFs providing mechanistic insights into population-level responses to conspecific density, and individual selection heterogeneity responses to anthropogenic and conspecific presence. Wildlife management might need to account for density-dependence when modelling or predicting species distributions, not only in cases of infanticide (Tortato et al. 2017) but also on the relative importance of density-dependence when sensitive population vital rates are directly affected, as previously observed in cases with wild dogs (Courchamp et al. 1999).

Proactive management plans should seek to maximize or maintain intact habitat to allow individual movement behaviors to persist, minimizing mortality risk for predators and livestock alike by giving predators the necessary security cover to hunt native prey species and protect young cubs. With rapidly shifting distributions and concentration in “safe” landscapes that may compromise population persistence, at the risk of creating attractive sinks whereby patches of locally high conspecific densities could introduce intraspecific strife in an otherwise protected landscape. Long-term management plans should account for this long-term risk and guard against otherwise “wildlife-friendly” working landscapes from becoming attractive sinks. Jaguar populations in these “secure” landscapes might be considered stable. Care should be taken, however, to continue monitoring these populations to track and mitigate potential deviations of population vital rates (i.e., survival; recruitment) due to the often ignored effects of density dependence.

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Table 4-1. Top conditional third order (home range level) RSF model with competing models including jaguar density as a possible fixed effect covariate for conditional use (use) and individual random effect (c\_IDjag), without interactions, without jaguar density, and null. The individual random effect was included in all models. Model selection criteria (degrees of freedom, df,  $\Delta$ AIC, and AIC weight,  $w_i$ ) are reported.

Third order (home range) RSF models	df	$\Delta$ AIC	$w_i$
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density + (jaguar density $\times$ cover) + (jaguar density $\times$ wild prey activity) + (jaguar density $\times$ cattle activity) + (jaguar density $\times$ river distance)	12	0	1
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density	8	209.81	0
use ~ cover + road distance + river distance + wild prey activity + cattle activity	7	410.11	0
Null, use ~ (1)	2	991.90	0

Cover = percent canopy cover (best-fit grain size = 500 m average);  
 Continuous river distance and road distance in meters (m);  
 Wild prey activity = relative activity index (scaled from 0:1; grain = 700 m pixel);  
 Cattle activity (scaled from 0:1; grain = 5 km average);  
 Jaguar density in individuals per 100 km<sup>2</sup> (grain = 5 km average).

Table 4-2. Top conditional fourth order (foraging level, daily movement scale = 5 km buffer) RSF model with competing models including jaguar density as a possible fixed effect covariate for conditional use (use) and individual random effect (c\_IDjag), without interactions, without jaguar density, and null. The individual random effect was included in all models. Model selection criteria (degrees of freedom, df,  $\Delta$ AIC, and AIC weight,  $w_i$ ) are reported.

Fourth order (daily movement) RSF models	df	$\Delta$ AIC	$w_i$
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density + (jaguar density $\times$ cover) + (jaguar density $\times$ wild prey activity) + (jaguar density $\times$ cattle activity) + (jaguar density $\times$ river distance)	12	0	1
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density	8	574.16	0
use ~ cover + road distance + river distance + wild prey activity + cattle activity	7	662.95	0
Null, use ~ (1)	2	3,989.02	0

Cover = percent canopy cover (best-fit grain size = 500 m average);  
 Continuous river distance and road distance in meters (m);  
 Wild prey activity = relative activity index (scaled from 0:1; grain = 700 m pixel);  
 Cattle activity (scaled from 0:1; grain = 5 km average);  
 Jaguar density in individuals per 100 km<sup>2</sup> (grain = 5 km average).

Table 4-3. Top conditional fourth order (foraging level, step length scale = 500 m) RSF models with competing models including jaguar density as a possible fixed effect covariate for conditional use (use) and individual random effect (c\_IDjag), without interactions, without jaguar density, and null. The individual random effect was included in all models. Model selection criteria (degrees of freedom, df,  $\Delta$ AIC, and AIC weight,  $w_i$ ) are reported.

Fourth order (step) RSF models	df	$\Delta$ AIC	$w_i$
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density + (jaguar density $\times$ cover) + (jaguar density $\times$ wild prey activity) + (jaguar density $\times$ cattle activity)	11	0	1
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density + (jaguar density $\times$ cover) + (jaguar density $\times$ wild prey activity) + (jaguar density $\times$ cattle activity) + (jaguar density $\times$ river distance)	12	1,871.57	0
use ~ cover + road distance + river distance + wild prey activity + cattle activity + jaguar density	8	2,130.05	0
use ~ cover + road distance + river distance + wild prey activity + cattle activity	7	2,184.93	0
Null, use ~ (1)	2	5,860.59	0

Cover = percent canopy cover (best-fit grain size = 500 m average);  
 Continuous river distance and road distance in meters (m);  
 Wild prey activity = relative activity index (scaled from 0:1; grain = 700 m pixel);  
 Cattle activity (scaled from 0:1; grain = 5 km average);  
 Jaguar density in individuals per 100 km<sup>2</sup> (grain = 5 km average).

Table 4-4.  $\beta$  coefficient estimates ( $\pm$  SE) for fixed effect on conditional use (use) and random effects (individual jaguar) at third order (home-range) and fourth order (daily foraging), for best-fit models (w/ jaguar density) and models without jaguar density (w/o jaguar density).

Coefficient	<i>Third order (home range)</i>		<i>Fourth order (daily foraging)</i>		<i>Fourth order (step foraging)</i>	
	w/ jaguar density	w/o jaguar density	w/ jaguar density	w/o jaguar density	w/ jaguar density	w/o jaguar density
<i>Fixed effect (use ~)</i>						
Constant	-0.80 (0.39)**	-0.65 (0.44)	-3.55 (2.49)	-3.60 (2.35)	-1.47 (0.11)***	-3.75 (0.14)***
Cover	-0.64 (0.03)***	-0.53 (0.03)***	-0.19 (0.03)***	-0.10 (0.03)***	-0.19 (0.03)***	-0.08 (0.03)***
Road distance	-0.36 (0.03)***	-0.34 (0.03)***	-0.24 (0.02)***	-0.21 (0.02)***	-0.20 (0.03)***	-0.19 (0.02)***
River distance	-0.25 (0.06)***	-0.30 (0.04)***	-0.32 (0.05)***	-0.15 (0.04)***	-0.47 (0.04)***	-0.54 (0.03)***
Wild prey activity	0.05 (0.03)	-0.05 (0.03)	0.07 (0.03)**	0.05 (0.03)*	0.06 (0.03)*	0.06 (0.03)**
Cattle activity	0.14 (0.16)	-0.72 (0.14)***	-11.22 (0.25)***	-8.78 (0.20)***	-16.31 (0.12)***	-9.51 (0.06)***
Jaguar density	0.20 (0.04)***		0.78 (0.05)***		2.96 (0.05)***	
Jaguar density:cover	0.27 (0.03)***		0.04 (0.03)		0.35 (0.04)***	
Jaguar density: wild prey activity	-0.03 (0.04)		-0.10 (0.04)***		0.01 (0.04)	
Jaguar density: cattle activity	0.75 (0.08)***		-1.98 (0.09)***		-8.06 (0.10)***	
Jaguar density: river distance	-0.16 (0.04)***		-0.39 (0.04)***			

Cover = percent canopy cover (best-fit grain size = 500 m average);  
 Continuous river distance and road distance in meters (m);  
 Wild prey activity = relative activity index (scaled from 0:1; grain = 700 m pixel);  
 Cattle activity (scaled from 0:1; grain = 5 km average);  
 Jaguar density in individuals per 100 km<sup>2</sup> (grain = 5 km average).

\* Significance level at 0.10; \*\* significance level at 0.05; \*\*\* significance level at 0.01

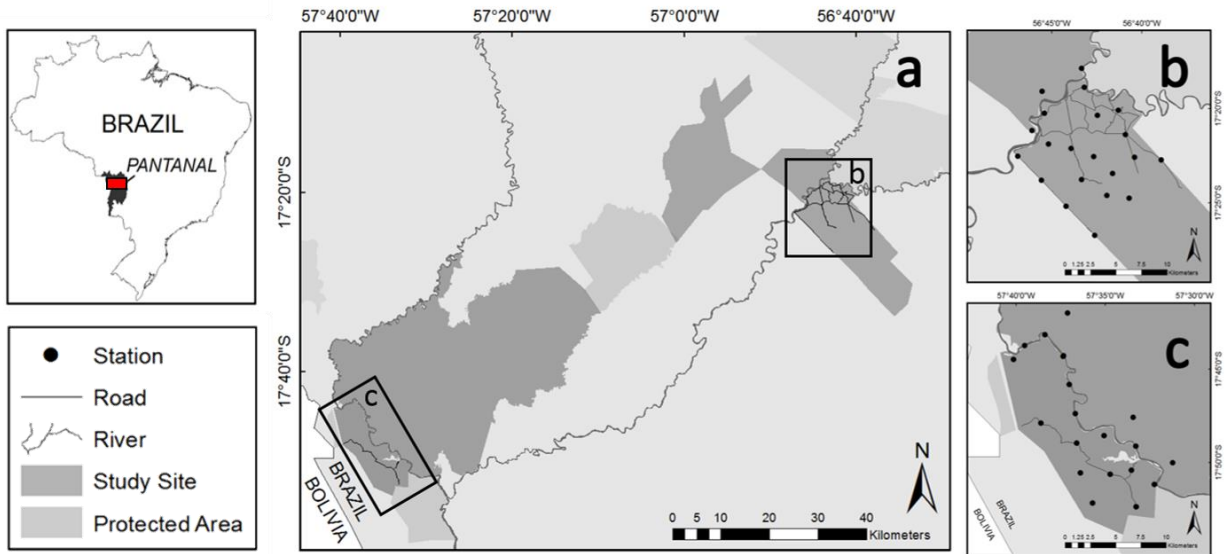


Figure 4-1. Study area (a), indicated on country map in red, located in the northern Brazilian Pantanal in states Mato Grosso (MT) and Mato Grosso do Sul (MS), with camera trap survey stations in (b) ranches (camera trap array covering 275.00 km<sup>2</sup> in Fazenda São Bento, MS and Fazenda Jofre Velho, MT) and (c) parks (camera trap array covering 300.00 km<sup>2</sup> in private reserve Acurizal, MS and Pantanal National Park-Matogrossense, MT, Brazil).



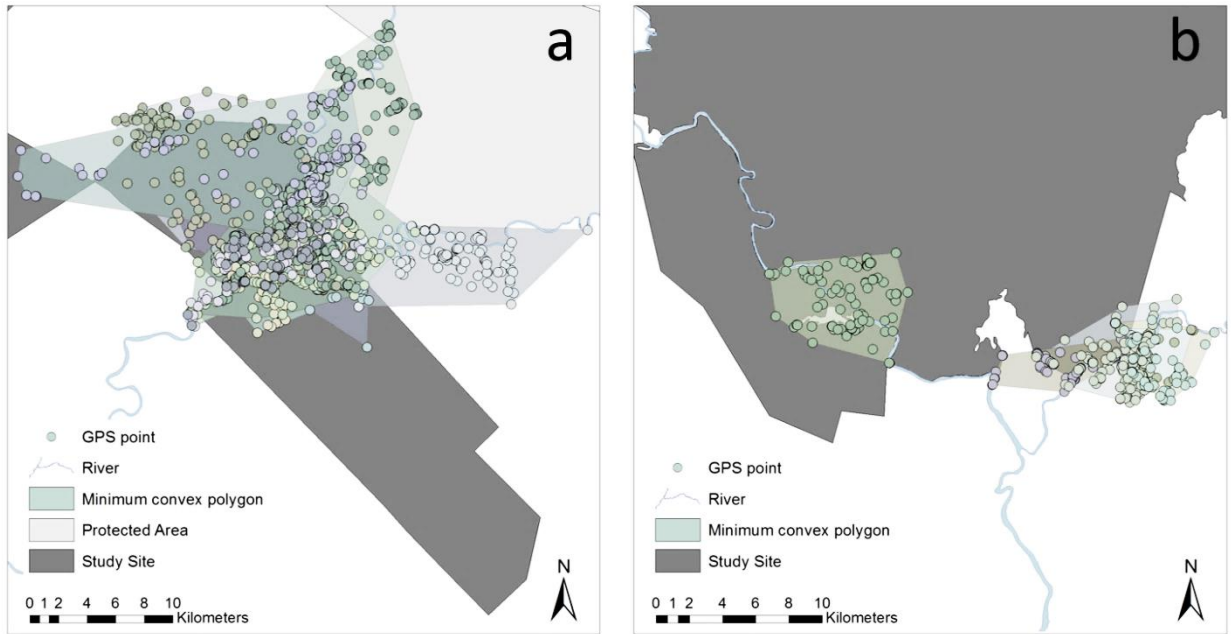


Figure 4-2. GPS points and minimum convex polygons of telemetered jaguars ( $n = 14$  individuals) monitored during the dry season (May – October 2011 – 2014) in the (a) ranches and (b) parks, Pantanal, Brazil.

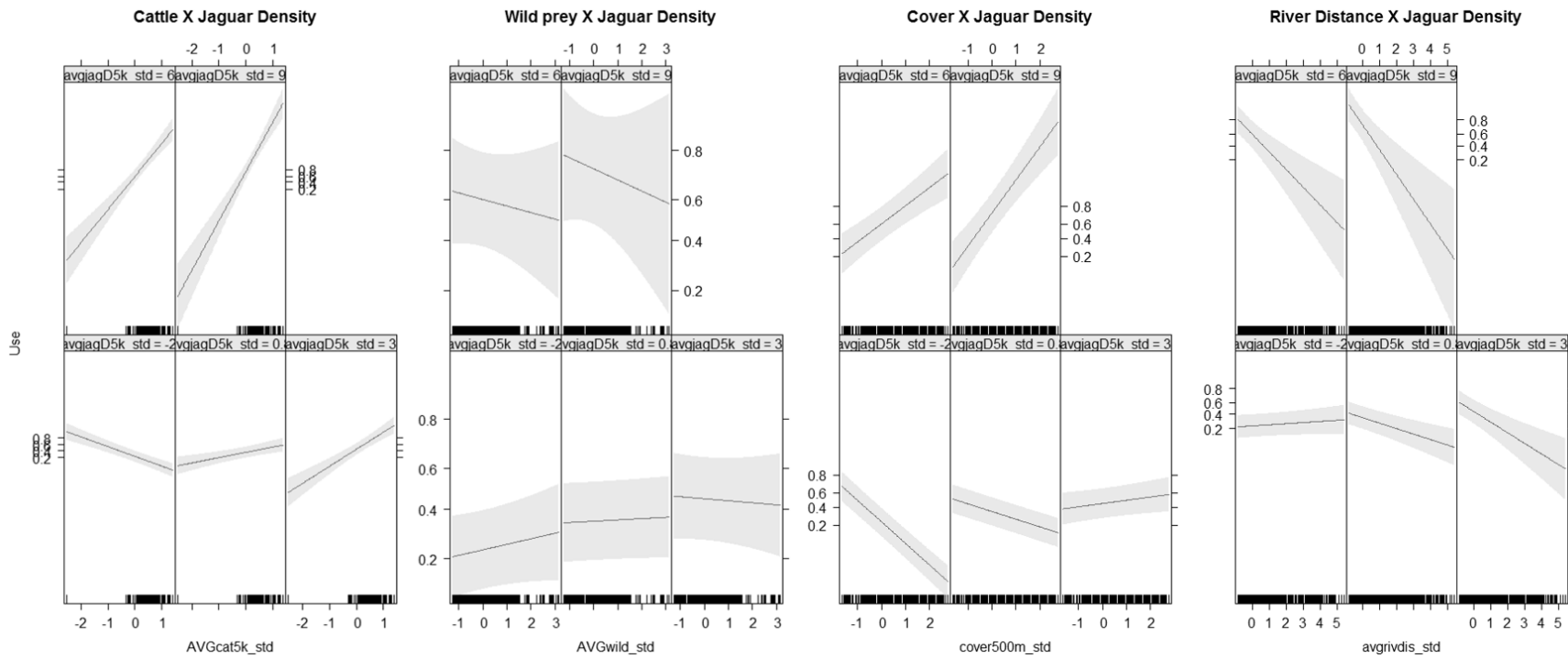


Figure 4-3. Partial effect slopes (black line) and 95% confidence intervals (shaded area) for use of habitat covariates including cattle, wild prey, cover, and river distance with interactions at low (a), mid-low (b), mid (c), mid-high (d) and high (e) jaguar densities at the home range scale. All covariates were standardized (z-score).

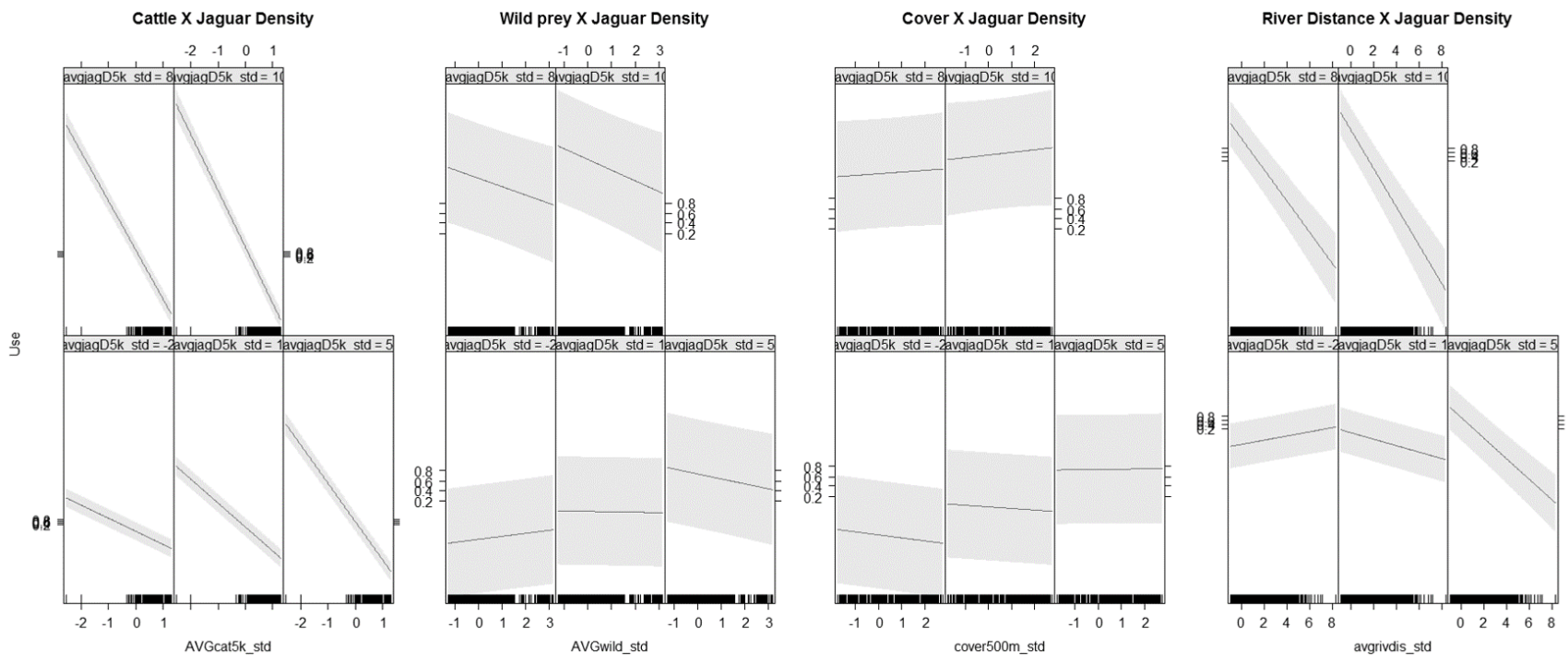


Figure 4-4. Partial effect slopes (black line) and 95% confidence intervals (shaded area) for use of habitat covariates including cattle, wild prey, cover, and river distance with interactions at low (a), mid-low (b), mid (c), mid-high (d) and high (e) jaguar densities at the daily movement (5 km) scale. All covariates were standardized (z-score).

Appendix 4-A. Correlation matrix of covariates and individual jaguar GPS data used for SSF analyses and correlation

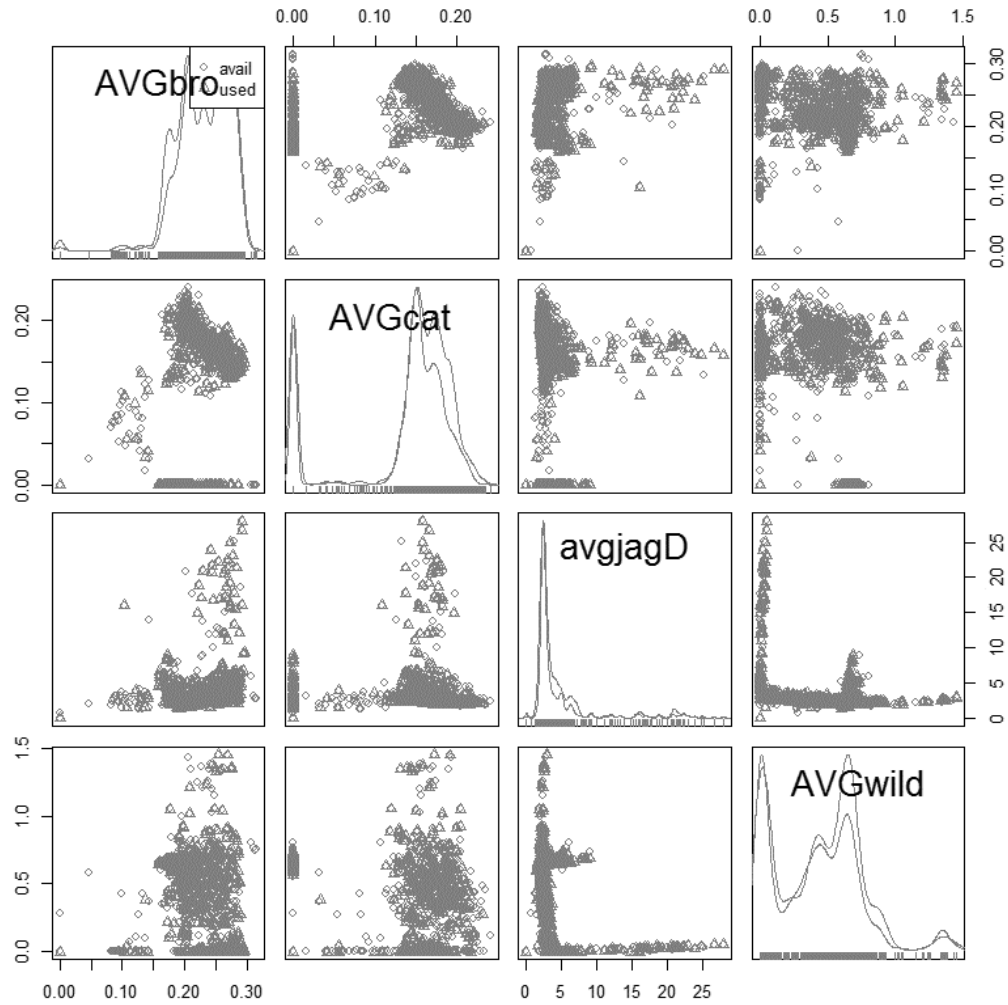


Figure 4-A1. Correlation matrix for subset of covariates included in conditional RSF analyses for telemetered jaguars, including relative activity index ( $RA_{ctI}$ ) for brocket deer (AVGbro), cattle (AVGcat), wild prey composite (AVGwild), and jaguar density (avgjagD). No covariates had Pearson's correlation ( $r$ ) values  $> 0.70$ .

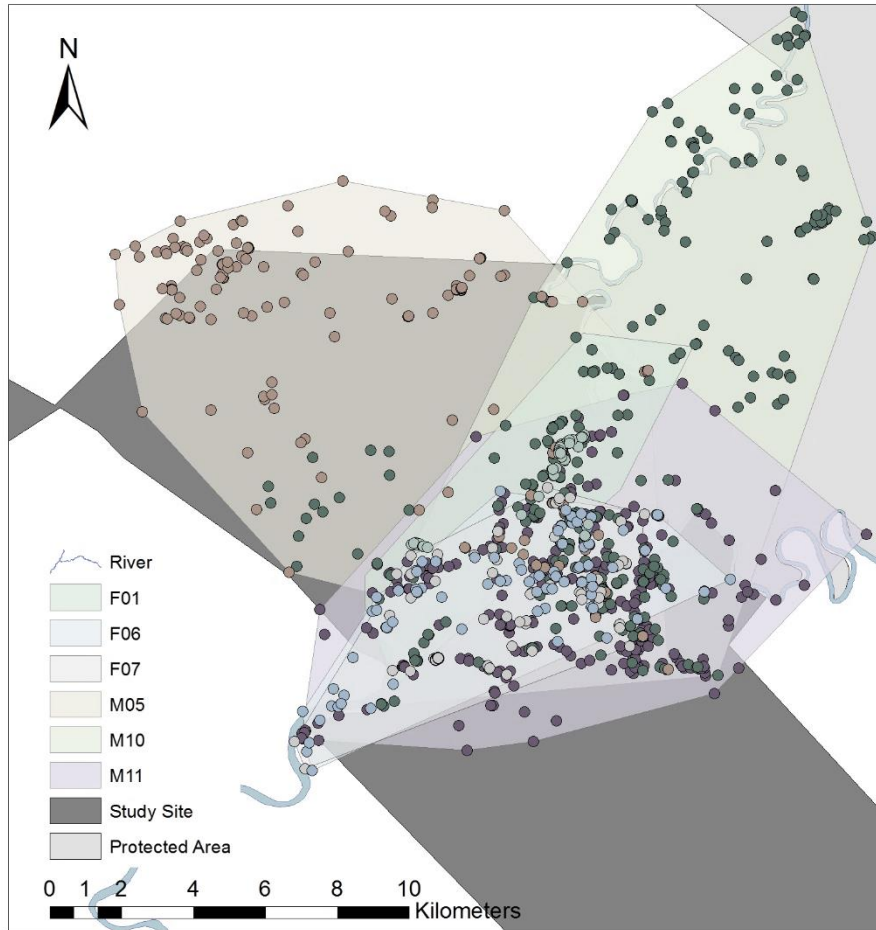


Figure 4-A2. Distribution of GPS point data and minimum convex polygons of telemetered individuals included in SSF analyses (F01, F06, F07, M05, M10, and M11) in the ranch complex, northern Pantanal, Brazil.

Appendix 4-B. GPS collar, covariate, and integrated step selection function (iSSF) model summary tables

Table 4-B1. Summary data for 15 collars deployed on 14 individual jaguars from 2011 - 2014 (M = male; F = female) including estimated ( $\pm$  SE) minimum convex polygon (MCP, km<sup>2</sup>), number of random points sampled per home range (sampling intensity of 0.0001 per m<sup>2</sup>), and average daily movement rate (km) for individuals included in third order RSF models. Individuals included in the step selection function (iSSF) analyses are indicated in bold.

Individual ID	Collar ID	Site	First GPS point (dd/mm/yyyy)	Final GPS point (dd/mm/yyyy)	Total points	MCP (km <sup>2</sup> )	Third order (# random points)	Average daily movement (km)
<b>M05</b>	<b>11160</b>	<b>Ranch</b>	<b>09/06/2013</b>	<b>13/10/2013</b>	<b>126</b>	<b>143.14</b>	<b>1431</b>	<b>5.28</b>
M07	8982	Ranch	26/06/2011	29/10/2011	142	80.57	806	5.27
M08	8983	Park	08/07/2011	04/10/2011	110	40.50	405	3.74
M09	8977	Park	02/07/2011	20/08/2011	28	-	-	-
<b>M10</b>	8991	Ranch	14/10/2011	13/05/2012	235	49.99	500	5.56
	<b>11158</b>	<b>Ranch</b>	<b>20/06/2013</b>	<b>23/12/2013</b>	<b>186</b>	<b>146.62</b>	<b>1466</b>	<b>6.56</b>
<b>M11</b>	<b>11157</b>	<b>Ranch</b>	<b>14/10/2012</b>	<b>23/10/2013</b>	<b>375</b>	<b>103.23</b>	<b>1032</b>	<b>4.83</b>
M12	11161	Ranch	21/06/2013	28/08/2014	72	162.91	1629	2.96
M15	15226	Ranch	11/07/2014	19/11/2014	378	140.66	-	-
<b>F01</b>	<b>7275</b>	<b>Ranch</b>	<b>16/10/2013</b>	<b>19/12/2013</b>	<b>79</b>	<b>35.61</b>	<b>356</b>	<b>1.44</b>
F02	8984	Park	08/07/2011	30/09/2011	72	18.52	185	2.47
F04	8988	Ranch	14/10/2011	19/11/2012	698	52.68	527	2.46
F05	8993	Ranch	19/10/2013	22/10/2014	133	21.89	219	5.65
<b>F06</b>	<b>11159</b>	<b>Ranch</b>	<b>15/10/2012</b>	<b>13/04/2013</b>	<b>205</b>	<b>42.73</b>	<b>427</b>	<b>6.03</b>
<b>F07</b>	<b>11162</b>	<b>Ranch</b>	<b>21/10/2013</b>	<b>29/01/2014</b>	<b>139</b>	<b>39.68</b>	<b>397</b>	<b>7.78</b>
Average total					191.00	77.05 (13.82)		4.62
Average M					168.42	108.45 (16.64)		4.89
Average F					221.11	35.19 (5.28)		3.90

Table 4-B2. Summary of ID (individual; collar) and biometric data (age in years; weight in kg) for 14 individual jaguars captured and collared from 2011 - 2014 (M = male; F = female). Individuals included in the step selection function (iSSF) analyses are indicated in bold.

Individual ID	Collar ID	Site	Age (years)	Weight (kg)
<b>M05</b>	<b>11160</b>	<b>Ranch</b>	<b>8</b>	<b>105.00</b>
M07	8982	Ranch	7	-
M08	8983	Park	8	100.00
M09	8977	Park	6	-
<b>M10</b>	8991	Ranch	10	110.00
	<b>11158</b>	<b>Ranch</b>	<b>12</b>	<b>106.00</b>
<b>M11</b>	<b>11157</b>	<b>Ranch</b>	<b>6</b>	<b>130.00</b>
M12	11161	Ranch	9	75.00
M15	15226	Ranch	8	-
<b>F01</b>	<b>7275</b>	<b>Ranch</b>	<b>9</b>	<b>61.30</b>
F02	8984	Park	10	65.00
F04	8988	Ranch	7	64.00
F05	8993	Ranch	11	93.00
<b>F06</b>	<b>11159</b>	<b>Ranch</b>	<b>8</b>	<b>70.00</b>
<b>F07</b>	<b>11162</b>	<b>Ranch</b>	<b>6</b>	<b>72.00</b>
Average total			9	87.61
Average M			8.25	104.33
Average F			8.50	70.88

Table 4-B3. Average ( $\pm$  SE) and equal intervals classification of covariates including percent canopy (low, intermediate low, intermediate high, high), jaguar density (individuals per 100km<sup>2</sup>; low, intermediate, high), wild prey, brocket deer, and cattle relative activity index (scaled 0:1; low, intermediate, high).

Covariate	Average (SE)	Low	Intermediate low	Intermediate	Intermediate high	High
Canopy	0.34 (0.20)	0 – 0.25	0.26 – 0.50	-	0.51 – 0.75	0.76 – 1.00
Jaguar density	4.49 (4.75)	0 – 2.50	-	2.51 – 5.00	-	$\geq 5.01$
Wild prey activity	0.41 (0.33)	0 – 0.25	0.26 – 0.50	-	0.51 – 0.75	0.76 – 1.00
Brocket deer activity	0.23 (0.04)	0 – 0.25	0.26 – 0.50	-	0.51 – 0.75	0.76 – 1.00
Cattle activity	0.14 (0.06)	0 – 0.25	0.26 – 0.50	-	0.51 – 0.75	0.76 – 1.00



Table 4-B4. Coefficients for iSSF models including covariate for conspecific density for telemetered individual jaguars in a ranch complex, northern Brazilian Pantanal. See Appendix 4-D (Tables 4-D1 to 4-D6) for model selection criteria.

Individual ID	Jaguar density	coef	exp(coef)	SE(coef)	z	Pr(> z )
F01	low	-	-	-	-	-
	intermediate	2.44	11.50	2.02	1.21	0.23
	high	1.28	3.60	2.11	0.61	0.55
F06	low	-	-	-	-	-
	intermediate	1.34	3.80	0.71	1.89	0.06
	high	2.51	12.25	0.61	4.14	<0.001
F07	low	-	-	-	-	-
	intermediate	-0.09	0.91	1.16	-0.08	0.94
	high	-0.64	0.53	1.08	-0.60	0.55
M05	low	-	-	-	-	-
	intermediate	-15.43	< 0.001	6,172.00	0.00	1.00
	high	-0.31	0.73	1.18	-0.27	0.79
M10	low	-	-	-	-	-
	intermediate	0.22	1.24	2.19	0.10	0.92
	high	-0.74	0.47	2.01	-0.37	0.71
M11	low	-	-	-	-	-
	intermediate	1.61	5.03	1.31	1.23	0.22
	high	-0.67	0.51	0.74	-0.91	0.37

Appendix 4-C. Density plots of step length and turn angle for best-fit individual jaguar models

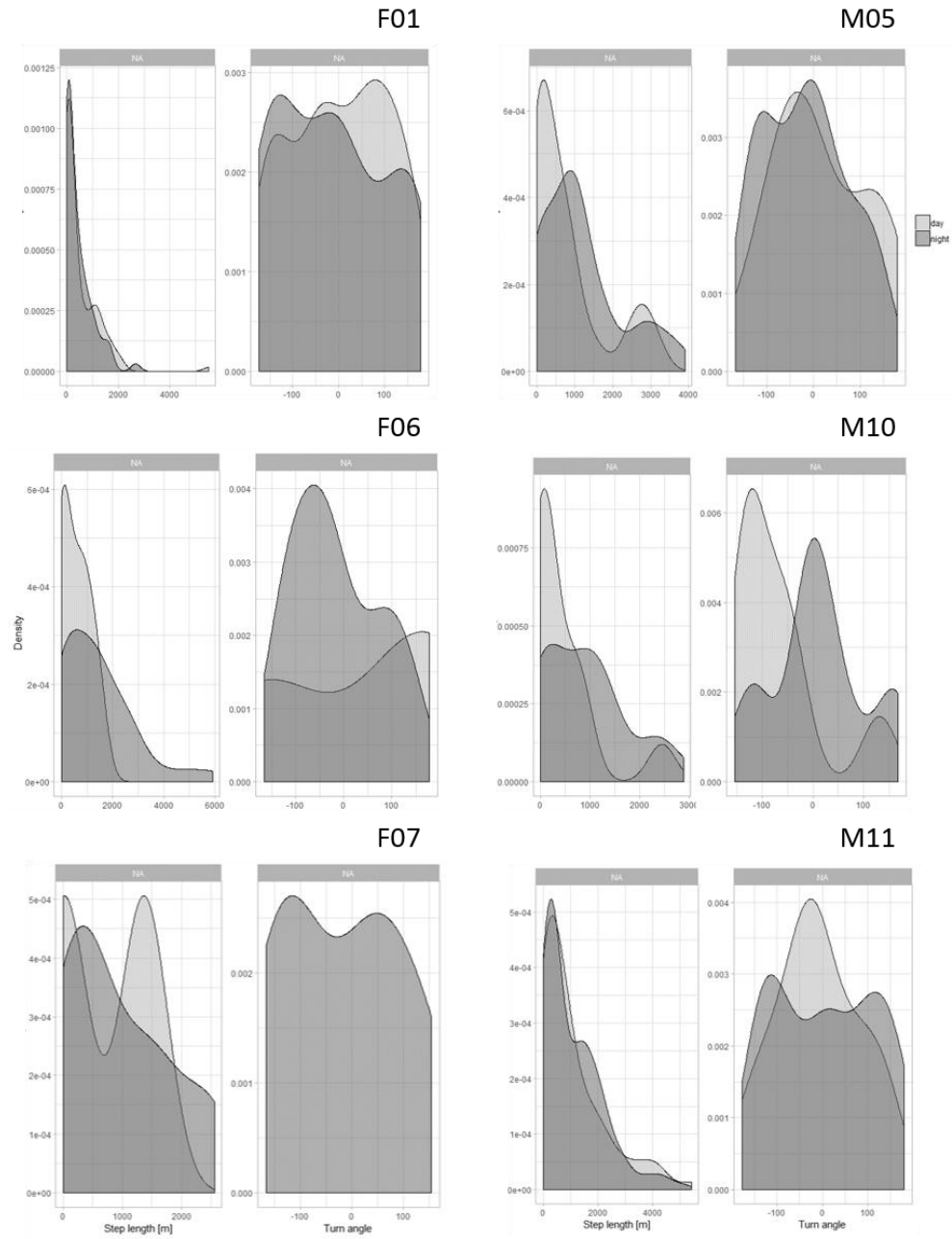


Figure 4-C1. Density plot analysis of diurnal and nocturnal trends in step length (left column, in m) and turn angle (right column) for selected telemetered individual jaguars in the ranch complex, northern Brazilian Pantanal.

F01

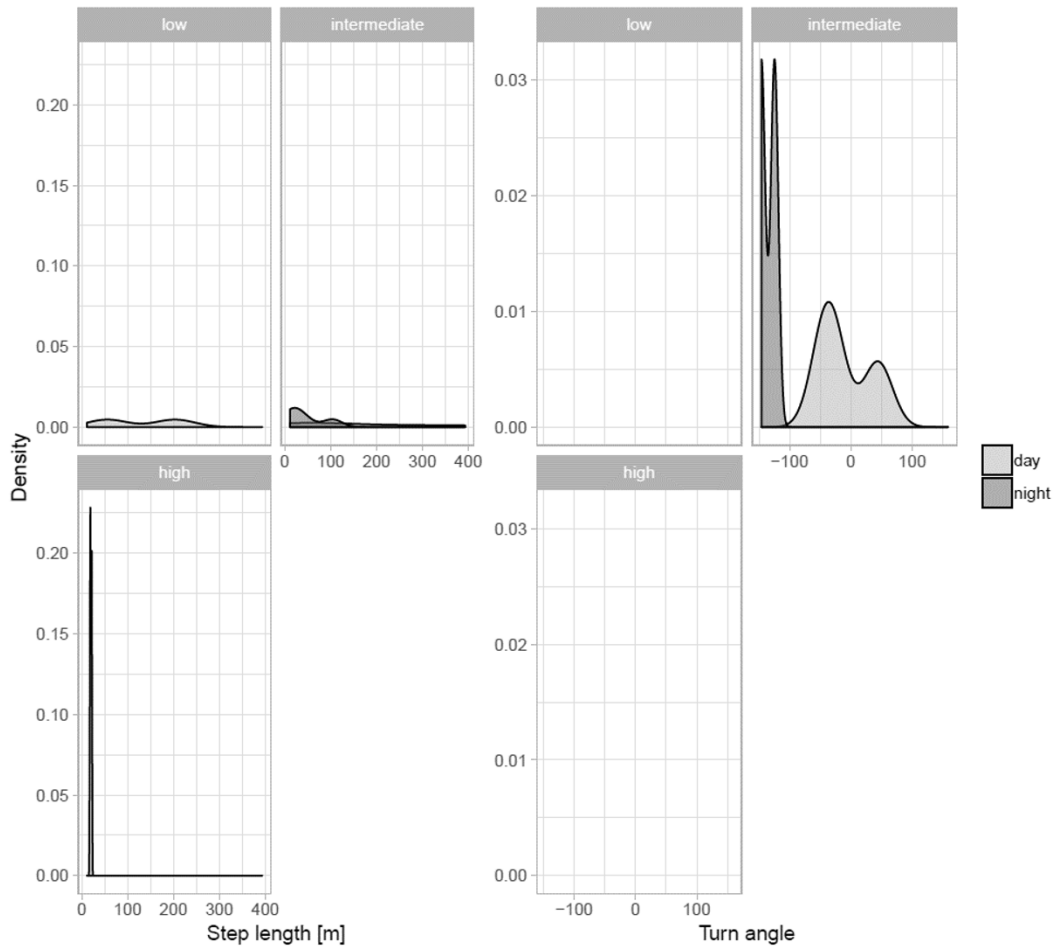


Figure 4-C2. Density plots of step length (in meters, left column) and turn angle (right column) as expected from the top model for jaguar F01 during the day (light grey; 06:00 – 17:59) and night (dark grey; 18:00 – 05:59; Signer et al. 2019) in areas with low, intermediate, and high conspecific density.

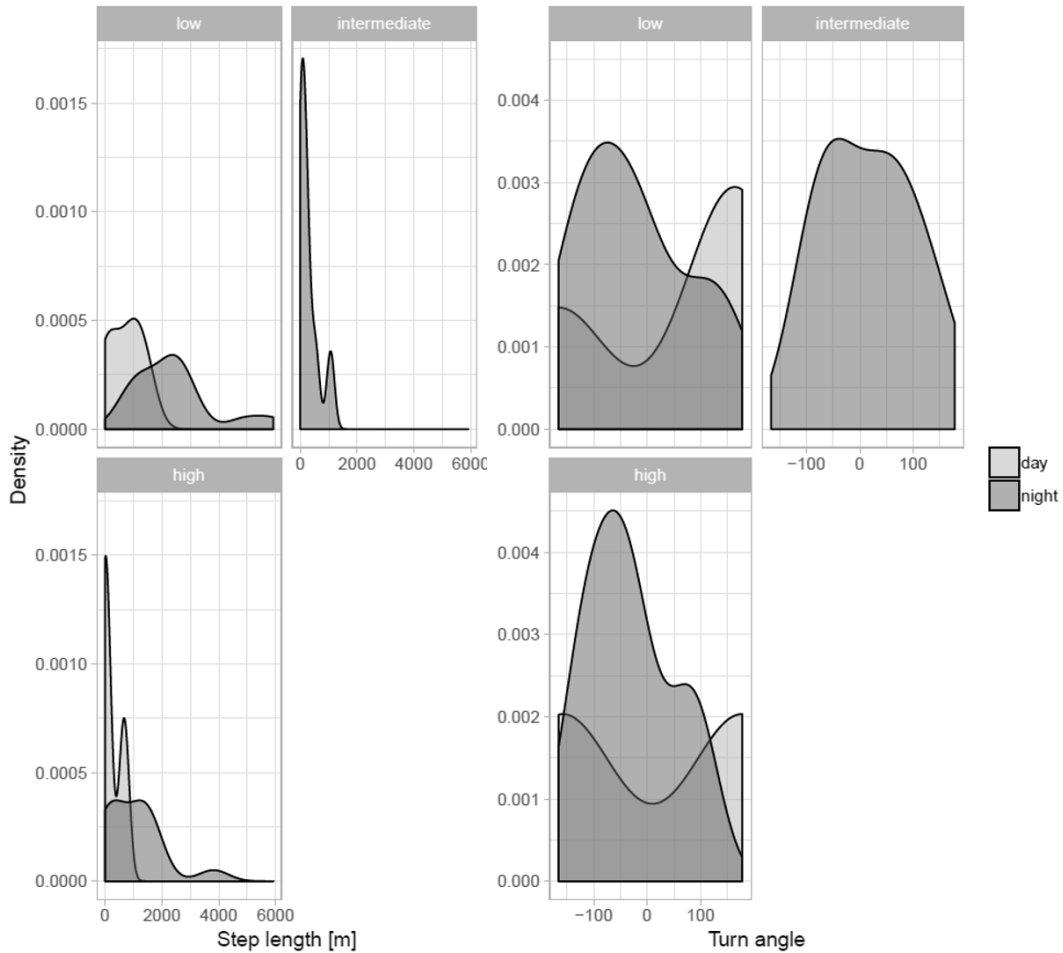


Figure 4-C3. Density plots of step length (in meters, left column) and turn angle (right column) as expected from the top model for jaguar F06 during the day (light grey; 06:00 – 17:59) and night (dark grey; 18:00 – 05:59; Signer et al. 2019) in areas with low, intermediate, and high conspecific density.

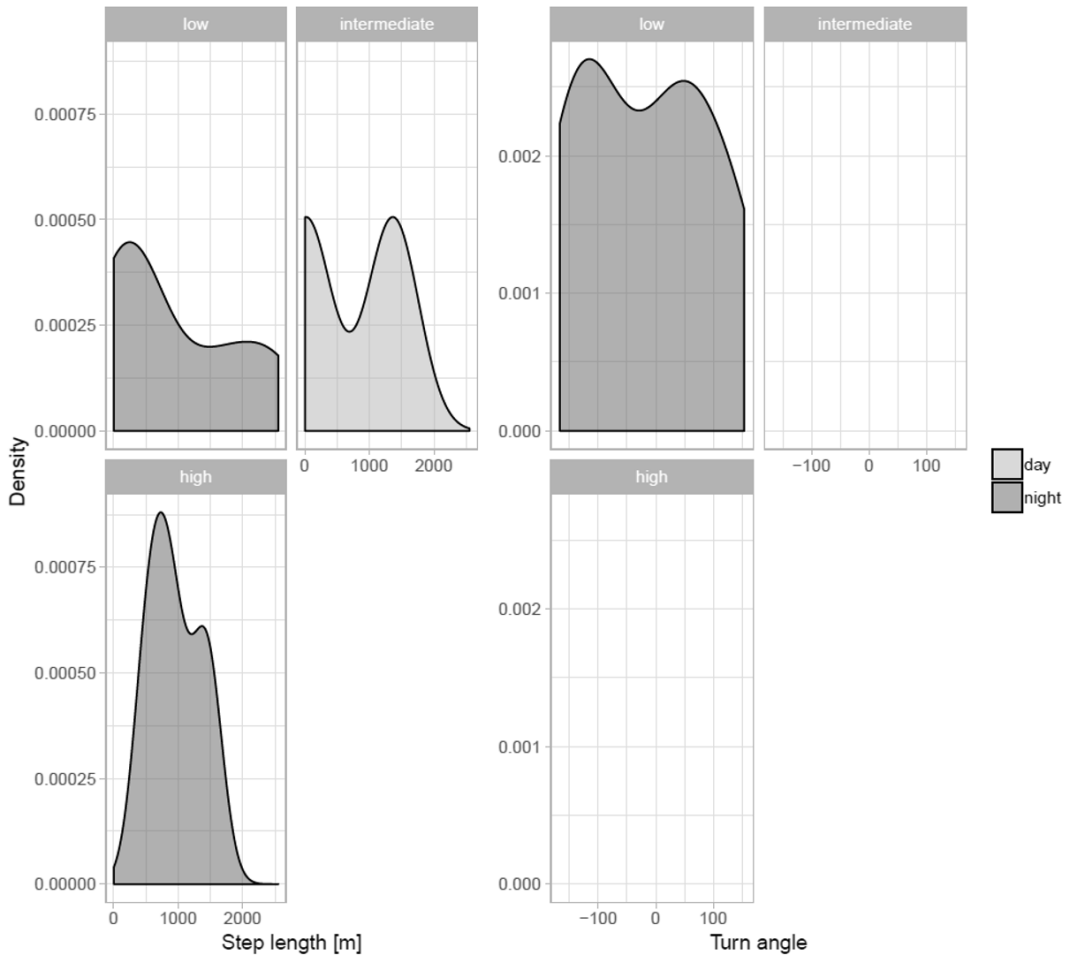


Figure 4-C4. Density plots of step length (in meters, left column) and turn angle (right column) as expected from the top model for jaguar F07 during the day (light grey; 06:00 – 17:59) and night (dark grey; 18:00 – 05:59; Signer et al. 2019) in areas with low, intermediate, and high conspecific density.

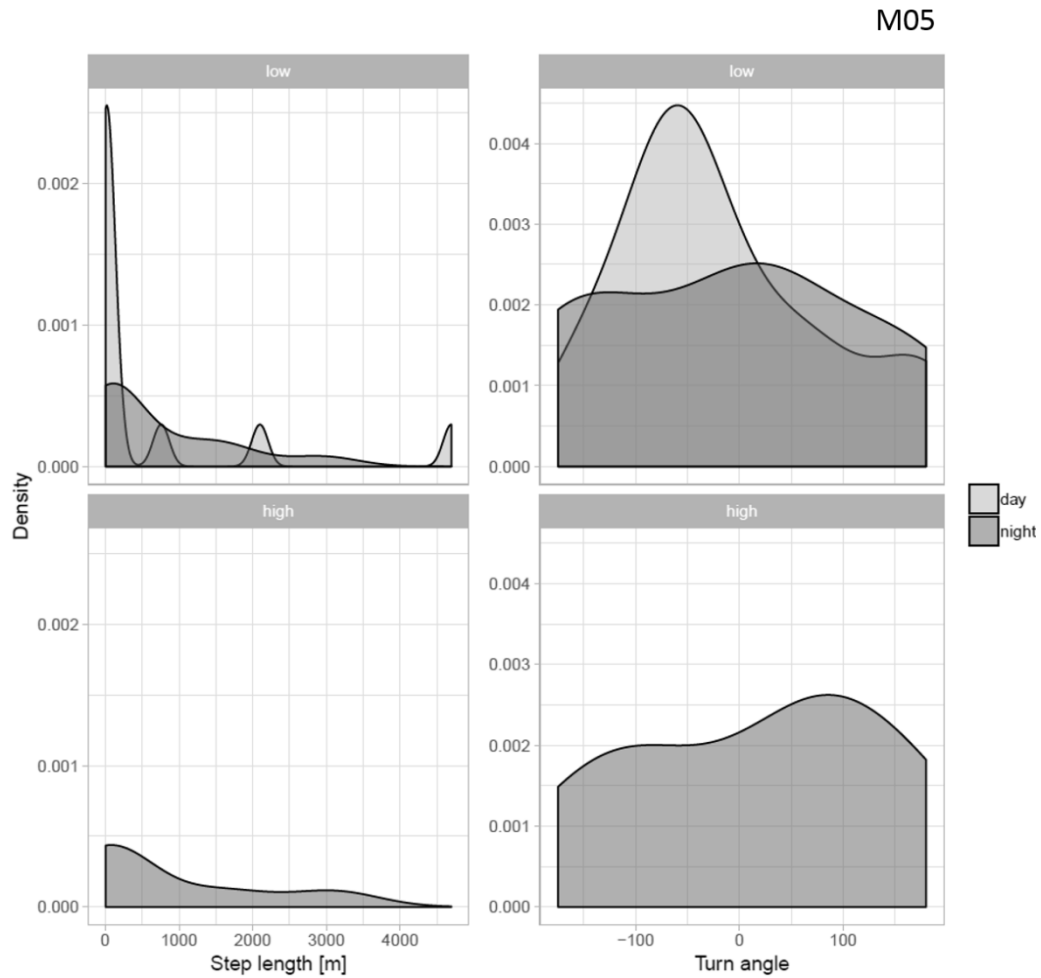


Figure 4-C5. Density plots of step length (in meters, left column) and turn angle (right column) as expected from the top model for jaguar M05 during the day (light grey; 06:00 – 17:59) and night (dark grey; 18:00 – 05:59; Signer et al. 2019) in areas with low, intermediate, and high conspecific density.

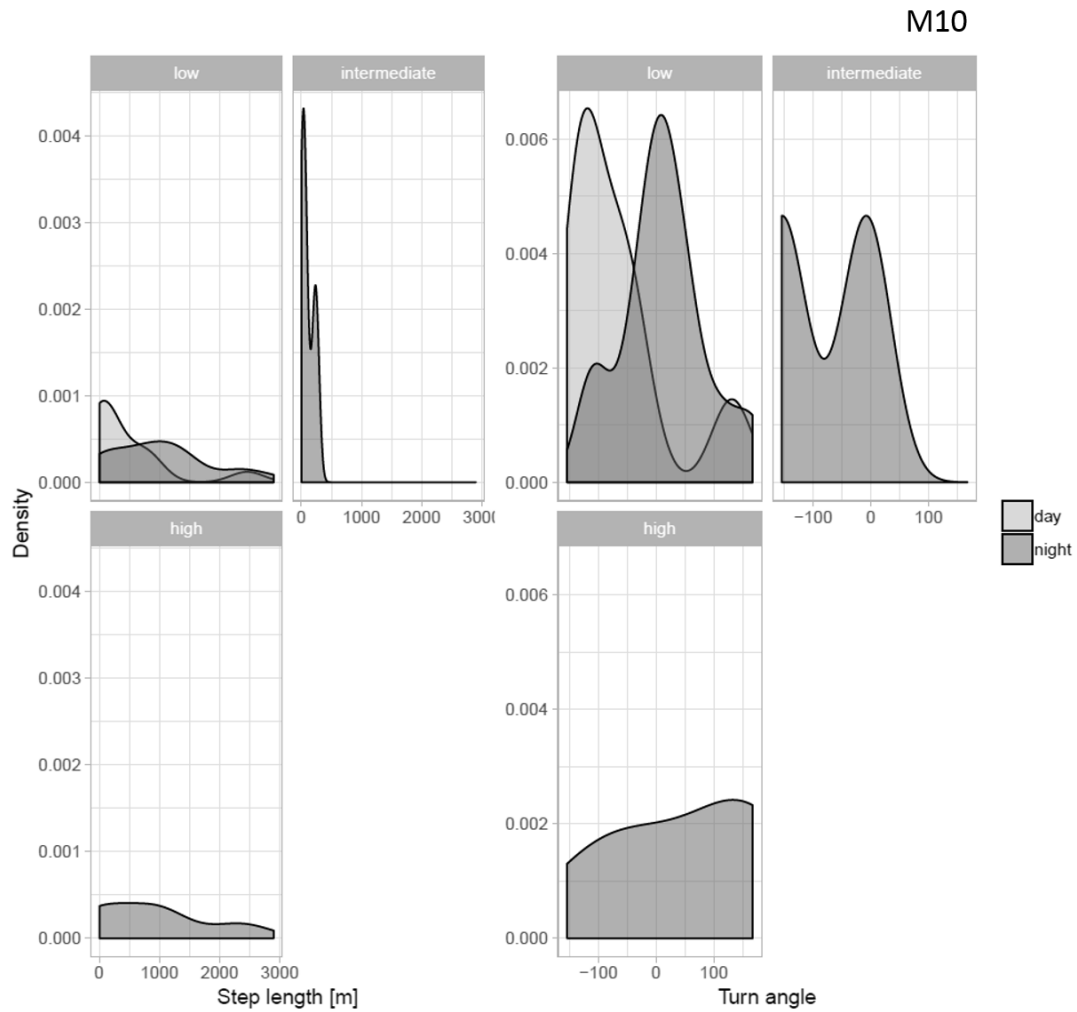


Figure 4-C6. Density plots of step length (in meters, left column) and turn angle (right column) as expected from the top model for jaguar M10 during the day (light grey; 06:00 – 17:59) and night (dark grey; 18:00 – 05:59; Signer et al. 2019) in areas with low, intermediate, and high conspecific density.

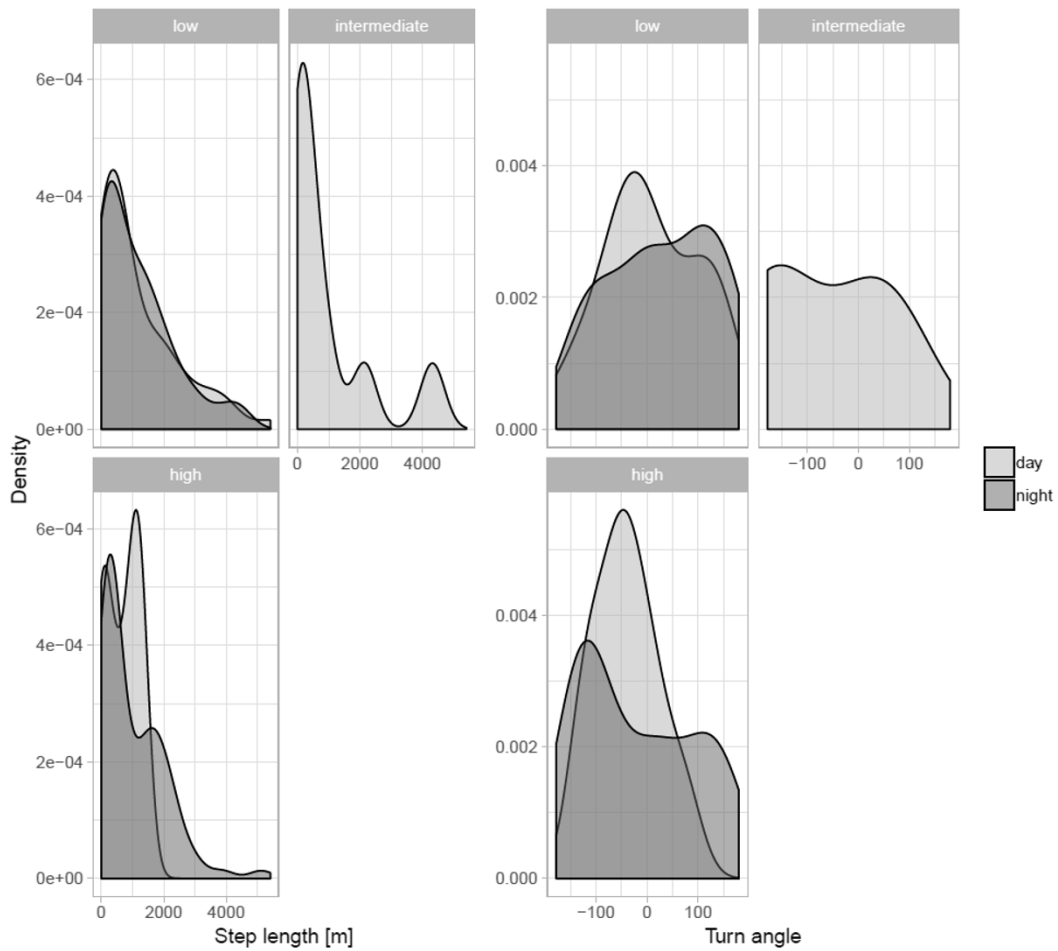


Figure 4-C7. Density plots of step length (in meters, left column) and turn angle (right column) as expected from the top model for jaguar M11 during the day (light grey; 06:00 – 17:59) and night (dark grey; 18:00 – 05:59; Signer et al. 2019) in areas with low, intermediate, and high conspecific density.



Appendix 4-D. Ranked iSSF models and model selection criteria for 6 telemetered individual jaguars in the ranch study site

Table 4-D1. Ranked models for female jaguar F01 hypotheses including cover, conspecific density, composite wild prey, and cattle indices on step strata, step length (log of step length, log\_sl), and turn angle (cosine of turn angle, cos\_ta), with reported degrees of freedom (df) and model selection criteria (AIC,  $\Delta$ AICc, and AICc weight ( $w_i$ )).

Hypothesis	Model	df	AICc	$\Delta$ AICc	$w_i$
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + cos ta + log_sl + strata(step_id_)	8	3.44	0	0.999
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + log_sl * cos_ta + strata(step_id_)	9	17.30	13.86	0.001
Cover	cover + cover:cos_ta + cover:log_sl + cos_ta + log_sl + strata(step_id_)	8	35.77	32.33	0
Cover	cover + cover:cos_ta + cover:log_sl + log_sl * cos_ta + strata(step_id_)	4	56.07	52.63	0
Jaguar density	jagdensity + strata(step_id_)	2	70.22	66.78	0
Cover	cover + strata(step_id_)	2	102.52	99.08	0
Wild prey	wild + strata(step_id_)	NA	NA	NA	NA
Wild prey	wild + wild:cos_ta + wild:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Wild prey	wild + wild:cos_ta + wild:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA
Cattle	cattle + strata(step_id_)	NA	NA	NA	NA
Cattle	cattle + cattle:cos_ta + cattle:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Cattle	cattle + cattle:cos_ta + cattle:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA

NA = failed to converge (infinite upper 95% confidence interval).

Table 4-D2. Ranked models for female jaguar F06 hypotheses including cover, conspecific density, composite wild prey, and cattle indices on step strata, step length (log of step length, log\_sl), and turn angle (cosine of turn angle, cos\_ta), with reported degrees of freedom (df) and model selection criteria (AIC,  $\Delta$ AICc, and AICc weight ( $w_i$ )).

Hypothesis	Model	df	AICc	$\Delta$ AICc	$w_i$
Jaguar density	jagdensity + strata(step_id_)	2	234.47	0	0.96
Cover	cover + strata(step_id_)	3	240.68	6.20	0.04
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + cos_ta + log_sl + strata(step_id_)	8	248.51	14.04	0.001
Cattle	cattle + strata(step_id_)	2	252.55	18.08	0
Wild prey	wild + strata(step_id_)	2	252.69	18.22	0
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + log_sl * cos_ta + strata(step_id_)	9	253.09	18.62	0
Cover	cover + cover:cos_ta + cover:log_sl + cos_ta + log_sl + strata(step_id_)	11	261.10	26.63	0
Cattle	cattle + cattle:cos_ta + cattle:log_sl + cos_ta + log_sl + strata(step_id_)	8	263.47	29.00	0
Wild prey	wild + wild:cos_ta + wild:log_sl + log_sl * cos_ta + strata(step_id_)	8	267.63	33.16	0
Cover	cover + cover:cos_ta + cover:log_sl + log_sl * cos_ta + strata(step_id_)	12	267.63	33.16	0
Cattle	cattle + cattle:cos_ta + cattle:log_sl + log_sl * cos_ta + strata(step_id_)	9	267.99	33.52	0
Wild prey	wild + wild:cos_ta + wild:log_sl + cos_ta + log_sl + strata(step_id_)	9	272.17	37.70	0

Table 4-D3. Ranked models for female jaguar F07 hypotheses including cover, conspecific density, composite wild prey, and cattle indices on step strata, step length (log of step length, log\_sl), and turn angle (cosine of turn angle, cos\_ta), with reported degrees of freedom (df) and model selection criteria (AIC,  $\Delta$ AICc, and AICc weight ( $w_i$ )).

Hypothesis	Model	df	AICc	$\Delta$ AICc	$w_i$
Jaguar density	jagdensity + strata(step_id_)	2	115.88	0	0.96
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + cos_ta + log_sl + strata(step_id_)	8	170.63	54.75	0.04
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + log_sl * cos_ta + strata(step_id_)	9	213.29	97.41	0.001
Cover	cover + cover:cos_ta + cover:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA
Cover	cover + cover:cos_ta + cover:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Cover	cover + strata(step_id_)	NA	NA	NA	NA
Wild prey	wild + strata(step_id_)	NA	NA	NA	NA
Wild prey	wild + wild:cos_ta + wild:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Wild prey	wild + wild:cos_ta + wild:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA
Cattle	cattle + strata(step_id_)	NA	NA	NA	NA
Cattle	cattle + cattle:cos_ta + cattle:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Cattle	cattle + cattle:cos_ta + cattle:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA

NA = failed to converge (infinite upper 95% confidence interval).

Table 4-D4. Ranked models for male jaguar M05 hypotheses including cover, conspecific density, composite wild prey, and cattle indices on step strata, step length (log of step length, log\_sl), and turn angle (cosine of turn angle, cos\_ta), with reported degrees of freedom (df) and model selection criteria (AIC,  $\Delta$ AICc, and AICc weight ( $w_i$ )).

Hypothesis	Model	df	AICc	$\Delta$ AICc	$w_i$
Cover	cover + cover:cos_ta + cover:log_sl + cos_ta + log_sl + strata(step_id_)	11	1325.91	0	0.29
Wild prey	wild + strata(step_id_)	2	1327.01	1.09	0.17
Cover	cover + strata(step_id_)	3	1327.30	1.39	0.15
Cattle	cattle + cattle:cos_ta + cattle:log_sl + cos_ta + log_sl + strata(step_id_)	8	1327.61	1.70	0.12
Cattle	cattle + strata(step_id_)	2	1328.16	2.25	0.09
Cover	cover + cover:cos_ta + cover:log_sl + log_sl * cos_ta + strata(step_id_)	12	1328.29	2.38	0.09
Wild prey	wild + wild:cos_ta + wild:log_sl + cos_ta + log_sl + strata(step_id_)	8	1329.83	3.92	0.04
Cattle	cattle + cattle:cos_ta + cattle:log_sl + log_sl * cos_ta + strata(step_id_)	9	1329.88	3.97	0.04
Wild prey	wild + wild:cos_ta + wild:log_sl + log_sl * cos_ta + strata(step_id_)	9	1332.11	6.20	0.01
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Jaguar density	jagdensity + strata(step_id_)	NA	NA	NA	NA

NA = failed to converge (infinite upper 95% confidence interval).

Table 4-D5. Ranked models for male jaguar M10 hypotheses including cover, conspecific density, composite wild prey, and cattle indices on step strata, step length (log of step length, log\_sl), and turn angle (cosine of turn angle, cos\_ta), with reported degrees of freedom (df) and model selection criteria (AIC,  $\Delta$ AICc, and AICc weight ( $w_i$ )).

Hypothesis	Model	df	AICc	$\Delta$ AICc	$w_i$
Wild prey	wild + strata(step_id_)	2	258.32	0	0.60
Cattle	cattle + strata(step_id_)	2	260.02	1.69	0.26
Jaguar density	jagdensity + strata(step_id_)	2	261.27	2.95	0.14
Wild prey	wild + wild:cos_ta + wild:log_sl + log_sl * cos_ta + strata(step_id_)	9	267.58	9.26	0.01
Cattle	cattle + cattle:cos_ta + cattle:log_sl + log_sl * cos_ta + strata(step_id_)	9	267.95	9.63	0.01
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + log_sl * cos_ta + strata(step_id_)	9	271.98	13.66	0.001
Cattle	cattle + cattle:cos_ta + cattle:log_sl + cos_ta + log_sl + strata(step_id_)	8	272.76	14.43	0
Wild prey	wild + wild:cos_ta + wild:log_sl + cos_ta + log_sl + strata(step_id_)	8	272.85	14.53	0
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + cos_ta + log_sl + strata(step_id_)	8	277.57	19.24	0
Cover	cover + cover:cos_ta + cover:log_sl + log_sl * cos_ta + strata(step_id_)	NA	NA	NA	NA
Cover	cover + strata(step_id_)	NA	NA	NA	NA
Cover	cover + cover:cos_ta + cover:log_sl + cos_ta + log_sl + strata(step_id_)	NA	NA	NA	NA

NA = failed to converge (infinite upper 95% confidence interval).

Table 4-D6. Ranked models for male jaguar M11 hypotheses including cover, conspecific density, composite wild prey, and cattle indices on step strata, step length (log of step length, log\_sl), and turn angle (cosine of turn angle, cos\_ta), with reported degrees of freedom (df) and model selection criteria (AIC,  $\Delta$ AICc, and AICc weight ( $w_i$ )).

Hypothesis	Model	df	AICc	$\Delta$ AICc	$w_i$
Cattle	cattle + strata(step_id_)	2	238.13	0	0.84
Wild prey	wild + strata(step_id_)	2	242.76	4.63	0.08
Jaguar density	jagdensity + strata(step_id_)	2	243.47	5.34	0.06
Cover	cover + strata(step_id_)	3	245.39	7.26	0.02
Cattle	cattle + cattle:cos_ta + cattle:log_sl + cos_ta + log_sl + strata(step_id_)	8	256.10	17.96	0
Cattle	Cattle + cattle:cos_ta + cattle:log_sl + log_sl * cos_ta + strata(step_id_)	9	259.68	21.55	0
Wild prey	wild + wild:cos_ta + wild:log_sl + cos_ta + log_sl + strata(step_id_)	8	260.47	22.34	0
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + cos_ta + log_sl + strata(step_id_)	8	261.47	23.34	0
Wild prey	wild + wild:cos_ta + wild:log_sl + log_sl * cos_ta + strata(step_id_)	9	264.49	26.36	0
Jaguar density	jagdensity + jagdensity:cos_ta + jagdensity:log_sl + log_sl * cos_ta + strata(step_id_)	9	265.02	26.89	0
Cover	cover + cover:cos_ta + cover:log_sl + log_sl * cos_ta + strata(step_id_)	11	270.07	31.93	0
Cover	cover + cover:cos_ta + cover:log_sl + cos_ta + log_sl + strata(step_id_)	12	276.66	38.53	0

Appendix 4-E. Example code for iSSF analyses conducted in R package ‘amt’ (Signer et al. 2019)

```
#####  
#iSSF ANALYSES: EXAMPLE CODE ‘amt’ (see Signer et al. 2019)  
#####  
setwd('/jaguars')  
getwd()  
  
library(amt)  
library(tidyverse)  
library(raster)  
library(sp)  
library(rgdal)  
library(lubridate)  
library(SDMTools)  
library(adehabitatMA)  
  
set.seed(123)  
  
#read in data from movebank.org or in movebank.org format, “jaguar.csv”  
# (data available in Morato et al. 2018)  
# here, tidyverse syntax: %>% = piping (indicates sequence of actions)...best  
# form to have space before, then start new line right after...  
dat <- read_csv('jaguar.csv') %>%  
  filter(!is.na('location-lat')) %>%  
  select(x = 'location-long', y = 'location-lat',  
         t = 'timestamp', id = 'tag-local-identifier') %>%  
  filter(id %in% c(7275, 11157, 11158, 11159, 11160, 11161, 11162))  
# all candidate individuals (sufficient data for iSSF) listed by collar ID
```

```

###
#RUN1: IND 7275
###

dat_1 <- dat %>% filter(id == 7275) #for ind 7275
head(dat_1)
tail(dat_1) #check data

#make a track with mk_track then transform coords
# (SAD 1969 21S EPSG = 5531 (UTM) and WGS84 = 4326 (geodetic))
dat_1 <- mk_track(dat_1, .x = x, .y = y, .t = t, crs = sp::CRS('+init = epsg:4326')) %>%
  transform_coords(sp::CRS('+init = epsg:5531'))
head(dat_1) #check data

dat_1 <- dat_1 %>% mutate(sl_ = step_lengths(.)) #first look at step length (sl_)
summary(dat_1$sl_)

#summarize distribution of time intervals
summarize_sampling_rate(dat_1)

#now check to see if location taken during night or day (time_of_day) and
# dawn / dusk (crepuscular)...
# adjusted hours(4) and mins(60) for fix rate...
# ...and only retain bursts of minimum # steps
stps <- track_resample(dat_1, rate = hours(4), tolerance = minutes(60)) %>%
  filter_min_n_burst(min_n = 3) %>% steps_by_burst() %>%
  time_of_day(include.crepuscule = TRUE) #set to true for dawn/dusk
str(stps) #inspect structure of stps
write.csv(stps, 'stps_ind7275.csv')

#example raster input: reclassified MODIS for
# canopy cover (1=0:25,2=26:50,3=51:75,4=76:100), 1=low, 2=ml, 3=mh, 4=high
cover <- raster('canopycover.tif')
hist(cover) #check data, confirm successful read-in

```



```

#Kernel density estimation (KDE)
kde1 <- hr_kde(dat_1)
hr_area(kde1)
get_crs(kde1)

#inspect track via interactive map in leaflet
inspect(dat_1, popup = 1:nrow(dat_1), cluster = FALSE)

#extract covariates at start, end of step
dat_1 %>% extract_covariates(cover)
dat_1 %>% steps %>% extract_covariates(cover)
dat_1 %>% steps %>% extract_covariates(cover, where = 'start')

#extract_covariates_along extracts the covariates along a straight line
# between the start and the end of step
p1 <- dat_1 %>% steps() %>% random_steps() %>%
  extract_covariates(cover) %>% # extract at the endpoint
  mutate(cover_path = extract_covariates_along(., cover)) %>%
  mutate(cover_path = purrr::map_dbl(cover_path, ~ mean(. == 1)))

#create random steps, extract cover covariates to steps, and create
# case_ object for models below...
ssf1 <- stps %>% random_steps(n = 100)
ssf1 <- ssf1 %>% extract_covariates(cover)
ssf1 <- ssf1 %>%
  mutate(canopy = factor(canopyrec11231, levels = 1:3, labels = c('low', 'intermediate', 'high')),
         cos_ta = cos(ta_),
         log_sl = log(sl_))

#now to fit clogit as wrapper around survival::clogit
# (SSF step by step manual p.3 of 7, Signer et al. 2019)
m0 <- ssf1 %>% fit_clogit(case_ ~ canopy + strata(step_id_))

```

```

m1 <- ssf1 %>% fit_clogit(case_ ~ canopy + canopy:cos_ta + canopy:log_sl + log_sl * cos_ta +
strata(step_id_))
m2 <- ssf1 %>% fit_clogit(case_ ~ canopy + canopy:cos_ta + canopy:log_sl + cos_ta + log_sl +
strata(step_id_))

summary(m0)
summary(m1)
summary(m2)

AICcmodels <- AICc(m0$model, m1$model, m2$model)

#...and plot output from best-fit cover model in density plot for
# step length and turn angle, day and night
# (see package 'amt' manual and vignette; Signer et al. 2019)
#PLOT 1 -----
p1 <- eda1 %>% select(canopy, tod = tod_end_, sl_) %>%
gather(key, val, -canopy, -tod) %>%
filter(key == 'sl_') %>%
ggplot(., aes(val, group = tod, fill = tod)) + geom_density(alpha = 0.5) +
facet_wrap(~ canopy, nrow = 2) +
xlab("Step length [m]") + theme_light() +
ylab("Density") +
theme(legend.title = element_blank())

p2 <- eda1 %>% select(canopy, tod = tod_end_, sl_, ta_) %>%
gather(key, val, -canopy, -tod) %>%
filter(key == "ta_") %>%
ggplot(., aes(val, group = tod, fill = tod)) + geom_density(alpha = 0.5) +
facet_wrap(~ canopy, nrow = 2) +
xlab("Turn angle") + theme_light() +
theme(legend.title = element_blank(),
axis.title.y = element_blank())

library(cowplot)

```

```
pg1 <- plot_grid(
  p1 + theme(legend.position = 'none'),
  p2 + theme(legend.position = 'none'), rel_widths = c(1,1)
)

leg <- get_legend(p1)
plot_grid(pg1, leg, rel_widths = c(1, 0.1))

ggsave('fig_ind7275_canopy-day-night.pdf', width = 20, height = 18, units = 'm')

###END###
```

## CHAPTER 5: CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Rangewide threats to the persistence of Neotropical wildlife include habitat loss, conflict and competition with livestock, and targeted hunting (Reyna-Hurtado and Tanner 2007, Briceno-Mendez et al. 2016), all of which contribute to the overall decline in remaining population strongholds in protected and unprotected areas. Many areas are not adequately protected against anthropogenic perturbations, and increasingly fragmented populations are threatening long-term viability. For many large carnivores, protected areas serve as population strongholds, and working landscapes along the borders form the front-line of carnivore conservation. While cattle ranches provide artificially high subsidies of protein, native prey populations may be suppressed or concentrated in remaining habitat patches. Understanding the mechanistic drivers of jaguar (*Panthera onca*) distribution is key to ensuring population persistence and providing important ecological baselines from which we can better inform management decisions for both land owners and governmental agencies (Sanderson et al. 2002).

In Chapter 2, I developed spatio-temporal prey activity surfaces derived from camera trap data and GIS layers to inform activity pattern and relative activity index (RA<sub>ctI</sub>) analyses. I found that, in the working landscape, species' activity patterns were not *significantly* different from the parks but did *trend* toward increased nocturnality, with reduced activity peaks and overall activity in daytime hours. Such patterns were also found on a global scale, with wildlife driven toward increased nocturnality in the face of human pressure (Gaynor et al. 2018). Jaguars tended to track spatial and temporal activity with native herbivores, although the felids still hunted cattle available throughout the ranch study site. Even with reduced mortality risk and some degree of habituation to humans through ecotourism (Tortato et al. 2017a), jaguars and main prey species avoided being active during peak levels of anthropogenic activity.

Where persecuted by poaching, diurnal species such as peccaries are at risk of overhunting. Hunting presents an especially important threat for herd-dwelling herbivores like peccaries – because peccaries travel in large groups, hunters can extirpate entire herds quite efficiently. In this study, large herds of white-lipped peccaries were historically recorded in the parks (Schaller 1983) but, due to hunting

pressure by ranchers before the area was officially protected in 1995, white-lipped peccaries were hunted to local extinction and even presently were not recorded in any of this study's camera trap surveys or transects (Devlin, unpub. data). White-lipped peccaries were therefore still considered locally extirpated from the parks. While large populations of white-lipped peccaries persist in the Pantanal, Amazon, and drier Cerrado regions of South America, in Mesoamerica this species has been extirpated from over 85% of its historic range (Altrichter et al. 2012). In such systems, the presence of feral buffalo (Alho et al. 2011) and / or feral pig (*Sus scrofa*) may actually alleviate poaching pressure from native wildlife species that are otherwise susceptible to overhunting in other parts of their range (Novaro et al. 2000, Desbiez et al. 2009). In hunted working landscapes, predators may therefore increasingly rely on solitary wild species like brocket deer and tapir, and predate upon resting livestock when cattle are left at night in unprotected pastures.

In Chapter 3, I evaluated the drivers of jaguar density by using spatially-explicit capture-recapture (SCR) and including covariates for food resources (prey activity derived from Chapter 1) and landscape covariates including security cover (derived from GIS layers). Female jaguars in the ranches were concentrated in higher quality habitat which provided greater security cover (canopy) and native prey biomass, presumably to meet the demands of cub rearing. Male jaguars tracked with females more consistently in the parks, though males in the ranches demonstrated greater variability in patchiness and greater risk-tolerance (Conde et al. 2010), with relatively high densities in open areas provisioned with livestock. The null results from the parks potentially reflect that our analyses did not capture the finer-scale attributes which likely influence jaguar distribution in areas with more uniform cover and prey availability. Overall, expected patterns of distribution broke down under the influence of working landscapes, whereby jaguar populations in the ranch complex exhibited patches of locally high jaguar densities due to provisioning of cattle, patchy distribution of prey, and resulted in increased conspecific aggression including otherwise rarely observed cases of infanticide at cattle carcasses (Tortato et al. 2017b).

Finally, in Chapter 4, I investigated the mechanistic drivers of population-level and individual jaguar movement using GPS data collected from telemetered individual jaguars to inform multi-scale resource selection function (RSF) and integrated step selection function (iSSF) models. Through this framework, I quantified the resource use and behavioral response of individuals to security cover (derived from GIS layers), dynamic availability of food resources (spatio-temporal prey biomass surfaces from Chapter 1), and conspecific density (derived from jaguar density surfaces in Chapter 2). The iSSF analyses teased apart individual behavioral responses to prevailing landscape conditions, with trends demonstrating that females tend to distribute across the landscape according to conspecific densities while males were more risk-tolerant and likely to move across open pastures with higher relative biomass of domestic livestock. Such results have important implications for working landscapes. By functionally demonstrating that resident individual jaguars will still move directly through areas of high cattle use at night, though avoiding daytime human activity, provides quantifiable metrics of risk and that pasture may not be as limiting to male movement (versus females). As females presumably must prioritize protecting young, vulnerable cubs, individual female jaguars tended to avoid areas with high conspecific densities. Functionally, then, I demonstrated that individual females may consistently be more sensitive to anthropogenic and density dependent perturbations with direct implications for prolonged population viability (Desbiez et al. 2012).

While I surveyed local populations using a robust study design (3 consecutive survey years per site), camera trap methodology and current analyses have limitations (Foster and Harmsen 2012, Tobler and Powell 2013). In this study, I neither measured seasonal (wet versus dry) trends in species distribution nor did I account for or include potential mortality events on neighboring ranches. Due to pronounced annual flooding events, the sampling period was limited to the dry season as I had improved accessibility to camera trap sites; sampling during this season also provided a stronger comparative lens for when water was a relatively limited resource. The park site was located in one of the only regions in the Pantanal that remained inundated throughout the entire year (Fortney et al. 2004) – such that landscape structure was likely driven by the persistent presence of permanent water bodies. The ranches, however, were more

similar to general conditions throughout the Pantanal, with marked drying and more limited availability of water and landscape structure primarily due to clear-cutting for pastures. Future research in the region should include sampling periods during both wet and dry seasons (as done by Cavalcanti and Gese 2010), to ground truth predictive models for prey and predator distribution and gain better inference into how and why local population densities may differ due to the response of prey species to these flooding events.

Though no predators were directly harvested on the ranch study site, camera trap records and local anecdotes indicated that neighboring ranches were engaged in unregulated harvesting or retaliatory action against predators, resulting in apparent but unconfirmed mortality events within the area defined by the habitat mask. Measuring the impacts of local anthropogenic mortality – while imperative – is a challenging task (Zimmermann et al. 2005). Hunting jaguars is considered a cultural and social norm throughout the Pantanal, and conservation efforts originating from outside the tight-knit community may be poorly received (Marchini and Macdonald 2012, Marchini and Crawshaw 2015).

For researchers to effectively communicate with ranchers or measure human-caused mortality of predators, long-term investment and engagement with key community members is critical (Marchini and Macdonald 2012). For example, efforts to reduce the lethality of working landscapes may increase human tolerance for predators by minimizing livestock loss (e.g. improved animal husbandry practices; Cavalcanti et al 2012, Quigley et al. 2015), generating revenue from their presence (e.g. ecotourism, Tortato et al. 2017a; and hunting, Novaro et al. 2000), or further supporting local communities that strive to coexist with predators (Jacobson and Robles 1992, Brewer 2002). Such efforts to reduce the mortality and direct persecution of large carnivores would, if successful, lead to a greater number of large carnivores surviving within these working landscapes, supporting metapopulation connectivity and long-term species persistence.

An important consideration of this study is that field surveys were limited to the dry season; therefore, the prior analyses do not reflect important wet season shifts in activity and distribution when dry land becomes more limiting (Polisar 2000). The approaches described herein should be extended to include monitoring over both wet and dry seasons (including shifting dynamics when cattle are moved

from lowland areas to higher, drier regions during the wet season; Polisar 2000, Hoogesteijn pers. comm.). Doing so would result in more reliable estimates of the seasonal drivers of relative activity (Michalski et al. 2015) and allow for greater precision when estimating density and population size, while also improving spatio-temporal predictions of species distributions across the dynamic landscape.

Across the mosaic of land use patterns throughout the Neotropics, the systems studied here followed what were considered “ideal” (protected area) and next-best alternative (wildlife-friendly ranch; Quigley et al. 2015, Tortato et al. 2017a) management techniques. Even still, wildlife will distribute to the intact forested areas and marginally shift circadian activity to avoid overlap with cattle – but not to as extreme a level as in other regions where overgrazing, clearcutting, and intensive poaching occurs (Briceno-Mendez et al. 2016). The accelerating expansion of high-intensity livestock operations in the Neotropics threatens the persistence of native species, especially in wildlife strongholds like the Pantanal and the Amazon (Wassenaar et al. 2007, McManus et al. 2016). Wildlife-friendly ranches that: (1) properly manage moderate herd levels of domestic ungulates so as not to overgraze pastures (Piana and Marsden 2014); (2) keep or integrate into the herd tamed buffalo; (3) maintain fencelines to keep cattle out of forest and riparian zones; (4) follow forestry regulations to support riparian and forest habitat; and (5) do not hunt native wildlife can actually facilitate the persistence of native herbivores (Polisar et al. 2003, Quigley et al. 2015, Larson et al. 2017). While recommendations are useful, in order to effectively mitigate conflict next steps must involve longer term monitoring and following up with landowners after a depredation event has occurred.

In other words, proper herd and landscape management can prevent habitat degradation and even assist conservation efforts in unprotected landscapes (Göldel et al. 2016, Larson et al. 2017), especially as surrounding regions become increasingly fragmented by more environmentally destructive land use practices like monocultures (e.g., palm oil; eucalyptus), mining, dams, and development. Current conservation and management efforts across the mosaic of working and protected landscapes must prioritize maintaining intact suitable habitat and prevent further habitat degradation (Scotter 1980, Quigley and Crawshaw 1992). With the rapid expansion of development, agriculture (i.e., expansive



industrial monocultures like soy, eucalyptus, and palm oil), and large-scale ranching comes the need to maintain habitat connectivity, and sustaining viable wildlife populations through alternative management techniques in unprotected areas is a very real, measurable, and persistent need in the world's increasingly fragmented landscapes.

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- Desbiez, A. L. J., K. Traylor-Holzer, B. Lacy, B. M. Beisiegel, C. Breitenmoser-würsten, D. A. Sana, E. A. Moraes, E. A. R. Carvalho Jr., F. De Lima, R. L. P. Boulhosa, R. C. De Paula, R. G. Morato, S. M. C. Cavalcanti, and T. G. de Oliveira. 2012. Population viability analysis of jaguar populations in Brazil. *CATnews Special Issue* 7:35–37.

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## CURRICULUM VITAE

### Allison L. Devlin

SUNY College of Environmental Science and Forestry  
1 Forestry Drive, Syracuse, NY 13210 USA  
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## Education

- Ph.D. Ecology** June 2019  
SUNY College of Environmental Science and Forestry, Syracuse, NY  
Major advisor: Dr. Jacqueline L. Frair  
*Dissertation: Drivers of jaguar (Panthera onca) distribution, density, and movement in the Brazilian Pantanal*
- M.A. Conservation Biology** 2008  
Columbia University, New York, NY  
*Thesis: Fecal corticoid and reproductive hormone concentrations in wild and captive jaguars (Panthera onca)*
- B.Sc. Animal Science, Magna cum Laude** 2006  
Cornell University, Ithaca, NY  
*Senior Research: Red maple (Acer rubrum) toxicity and vitamin E supplementation in domestic horses (Equus caballus)*

## Analyses and Techniques

### Modelling / Statistical

Spatially-explicit capture-recapture (maximum likelihood; Bayesian); classical mark-recapture; resource selection function / step selection function; occupancy; activity pattern; relative activity and abundance; biomass; map algebra

### Laboratory (scat samples)

#### *Hormonal assays*

Enzyme-linked immunosorbent assay (ELISA): cortisol; corticosterone; testosterone; estradiol hormone extraction and analysis

#### *Genetics*

DNA extraction; PCR; sequencing; sexing; microsat (Cytb; PON16S rRNA); 590bp mtDNA

## Field

### *Tracking and surveys*

Telemetry (GPS, VHF collars and tracking / triangulation); live capture campaigns using soft-hold footsnare; aerial surveys; camera trap surveys; line transects; habitat plots

### *Scat sample collection*

Certified scat detection dog handler (PackLeader Dog Training, Gig Harbor, WA)

## Software

R packages: secr; amt; adehabitat; SPACECAP; RMark; overlap; activity; ggplot2; tidyverse; WinBUGS; JAGS; ArcGIS; Geospatial Modelling Environment; Fragstats; PRESENCE; MARK; DISTANCE; GPSPlus; GPS TrackMaker; SEQUENCHER; Microsoft Excel, Word, Access, Powerpoint; Google Earth Engine

# Professional Experience

**Post-Doctoral Research Associate** 2019–present

University of Montana, Missoula, MT / Panthera, New York, NY

*Design, implement, and analyze results from in situ experiments mitigating jaguar-livestock predation in broader Human-Wildlife Conflict program*

**Research Associate** 2016–2019

Jaguar Program, Panthera, New York, NY

*Initiate designs and implementation of anti-predation experiments in Pantanal Jaguar Project; participate in local, regional, national, and international outreach materials and media; cultivate collaboration with key projects in Brazil*

**Senior Research Aide** 2016

SUNY ESF / New York State Department of Environmental Conservation, Syracuse, NY  
*River otter (*Lontra canadensis*) occupancy in NYS Region 9*

**Graduate Assistant** 2016

Department of Environmental & Forest Biology, SUNY ESF, Syracuse, NY

*Database management of graduate program applicants and undergraduate program assessment*

**Instructor** 2014

Department of Environmental & Forest Biology, SUNY ESF, Syracuse, NY

*Applied Wildlife Science (EFB 491 / EFB 796)*

## Graduate Teaching Assistant

Department of Environmental & Forest Biology, SUNY ESF, Syracuse, NY

– *Principles of Genetics (EFB308)* 2014

– *Applied Wildlife Science (EFB 491 / EFB 796)* 2012–2013

– *Introduction to Conservation Biology (EFB 413)* 2011

– *Problem Solving in Conservation Biology (EFB 419)* 2011

**Undergraduate Teaching Assistant**

Department of Animal Science, Cornell University, Ithaca, NY

– *Animal Behavior II (ANSC 4980)* 2006– *Exotic Animal Nutrition (ANSC 4980)* 2005**Research Assistant**

2005–2006

Department of Zoology, Cornell University College of Veterinary Medicine, Ithaca, NY

*Histochemical analysis of type I and II muscle fibers for research on: guinea fowl locomotion (stipend from Harvard University); thumbs of human stroke victims; and equine neck musculature***Field Research Training**

2010

Teton Cougar Project, Panthera / Craighead Beringia South, Kelly, WY

*GPS / VHF telemetry, aerial surveys, and kill site searches of cougar (Puma concolor)***Field Research Assistant**

2005

Big Cats Program, Wildlife Conservation Society, Cockscomb Basin Wildlife Sanctuary, Belize

*Camera trap surveys; transects; scat collection; meet with local private landowners and ranchers in assistance of PhD research conducted by Dr. Rebecca Foster***Mammal Keeper Intern**

2004

Mammal Department, Bronx Zoo, Wildlife Conservation Society, Bronx, NY

**Wild Asia Animal Show Presenter**

2003, 2004

Bronx Zoo, Wildlife Conservation Society, Bronx, NY

**Animal Keeper**

2002

Children's Zoo, Bronx Zoo, Wildlife Conservation Society, Bronx, NY

**Veterinary / Emergency Surgical Assistant**

– Flannery Emergency Animal Hospital, New Windsor, NY 2007–2008

– Goosepond Animal Hospital, Monroe, NY 2001–2002

**Peer-reviewed publications**Hofman, M., [...], **A. L. Devlin**, et al. 2019. Right on track? Performance of satellite telemetry in terrestrial wildlife research. PLoS ONE 14:e0216223.Santos, P.M., [...], **A.L. Devlin**, et al. 2019. Neotropical *Xenarthrans*: a data set of occurrence of xenarthran species in the Neotropics. Ecology 100:e02663.Morato, R. G., J. J. Thompson, [...], **A. L. Devlin**, et al. 2018. Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. Ecology 99:1691.

\*May Jr., J., H. B. Quigley, R. Hoogesteijn, P. G. Crawshaw Jr., F. R. Tortato, **A. L. Devlin**, R. Carvalho Jr., R.G. Morato, L.R. Sartorello, L.E. Rampin, M. Haberfeld, R. C. de Paula, and J. J. Zocche. 2017. Mercury content in the fur of jaguars (*Panthera onca*) from two areas under different levels of gold mining impact in the Brazilian Pantanal. *Annals of the Brazilian Academy of Sciences*, Centennial edition 90:2129–2139.

\**Documentary in production. 2018. MapaBiomass, SP, Brazil*

Tortato, F. R., **A. L. Devlin**, R. Hoogesteijn, J. May, J. Frair, P. G. Crawshaw, T. Izzo, and H. B. Quigley. 2016. Infanticide in a jaguar (*Panthera onca*) population - does the provision of livestock carcasses increase the risk? *acta ethologica* 20:69–73.

Tortato, F. R., J. Bonanomi, **A. L. Devlin**, and R. Hoogesteijn. 2013. Interspecific association between Collared Peccaries (*Pecari tajacu* Linnaeus, 1758 - Tayassuidae) and Azara's Capuchin (*Sapajus cay* Illiger, 1815 - Cebidae) in the Pantanal, Brazil. *Suiform Soundings* 12:17–18.

## Manuscripts in review / in prep

Rampim, L. E., L. Sartorello, C. E. Fragoso, M. Haberfeld, and **A. L. Devlin**. *In review*. Antagonistic interactions between predator and prey: mobbing of jaguars (*Panthera onca*) by white-lipped peccaries (*Tayassu pecari*). *acta ethologica*.

Riberio, B., [...], **A. L. Devlin**, et al. *In review*. Neotropical alien mammals: a dataset of occurrence and abundance of alien mammals in the Neotropics. *Ecology*.

Tortato, F. R., **A. L. Devlin**, R. L. P. Bolhousa, R. Hoogesteijn. *Submitted*. Where is the cat? Relative rarity of *Puma yagouaroundi*, *Leopardus pardalis*, *Leopardus guttulus*, and *Leopardus colocolo* in the Pantanal of Brazil. *Mammalian Biology*.

**Devlin, A. L.**, J. L. Frair, J. P. Gibbs, L. T. B. Hunter, J. B. Cohen, F. R. Tortato, R. H. Hoogesteijn, H. B. Quigley, and P. G. Crawshaw Jr. *In prep*. Influence of domestic ungulates on native herbivores in non-hunted landscapes.

**Devlin, A. L.**, J. L. Frair, J. P. Gibbs, L. T. B. Hunter, J. B. Cohen, F. R. Tortato, R. H. Hoogesteijn, H. B. Quigley, and P. G. Crawshaw Jr. *In prep*. Drivers of predator density in a dynamic landscape.

**Devlin, A. L.**, J. L. Frair, J. P. Gibbs, L. T. B. Hunter, J. B. Cohen, F. R. Tortato, R. H. Hoogesteijn, H. B. Quigley, and P. G. Crawshaw Jr. *In prep*. Density-dependent behavior of a solitary apex predator.

**Devlin, A. L.**, R. H. Hoogesteijn, F. R. Tortato, et al. *In prep*. Preventing predation: experimenting with predator-deterrent techniques in working cattle ranches.

Hayward, M. W., [...], **A. L. Devlin**, et al. *In prep.* Effects of apex predators on mesopredator use of tracks.

Harmsen, B. J., [...], **A. L. Devlin**, et al. *In prep.* Rangewide distribution of jaguarundi (*Herpailurus yagouaroundi*).

Tortato, F. R., **A. L. Devlin**, R. H. Hoogsteijn, W. Jędrzejewski, et al. *In prep.* Social behavior and formation of male coalitions in solitary apex predators.

## Popular Publications

Hoogsteijn, R. H., F. R. Tortato, and **A. L. Devlin**. 2019. Introducing the Jaguar M.F. Flash: Pt 1. Panthera Field Notes Blog. <https://www.panthera.org/blog/2019/02/11/introducing-jaguar-mf-flash-pt-1>.

**Devlin, A. L.** 2017. Why Panthera's School is Working in the Brazilian Pantanal. Panthera Journey of the Jaguar / Panthera Field Notes Blog. <https://www.journeyofthejaguar.org/entry/pantheras-school-working-brazilian-pantanal/>; <https://www.panthera.org/blog/2017/12/12/why-pantheras-school-working-pantanal>.

**Devlin, A. L.** 2016. Brazil's Jaguar Power: Floods & Feuds. Cover Feature, BBC Wildlife Magazine, September 2016:20–26.

Tortato, F. R., **A. L. Devlin**, and P. G. Crawshaw Jr. 2015. Um rodízio para as onças. O Eco: Rastro de Onca. [www.oeco.org.br/blogs/rastro-de-onca/28928-um-rodizio-para-as-oncas/](http://www.oeco.org.br/blogs/rastro-de-onca/28928-um-rodizio-para-as-oncas/).

Crawshaw, P. G. and **A. L. Devlin**. 2014. Acurizal vista com a mente (Parte I). O Eco: Rastro de Onca. [www.oeco.org.br/blogs/rastro-de-onca/28528-acurizal-vista-com-a-mente-parte-i/](http://www.oeco.org.br/blogs/rastro-de-onca/28528-acurizal-vista-com-a-mente-parte-i/).

Crawshaw P. G. and **A. L. Devlin**. 2014. Acurizal vista com o coração (Parte II). O Eco: Rastro de Onca. [www.oeco.org.br/blogs/rastro-de-onca/28545-acurizal-vista-com-a-coracao-parte-ii/](http://www.oeco.org.br/blogs/rastro-de-onca/28545-acurizal-vista-com-a-coracao-parte-ii/).

Teixeira, A. and P. Broggi. 2014. Felinos: A Luta pela Sobrevivência. Abook - Neoânima Comunicação, São Paulo, SP, Brazil. Revision of Text: D. Faria, P. G. Crawshaw Jr. and **A. L. Devlin**.

**Devlin, A. L.** 2008. Scat dog project in Cockscomb Basin Wildlife Sanctuary (CBWS). Belize Audubon Society 39:10–11.

**Devlin, A. L.** 2008. Fecal corticoid and reproductive hormone concentrations in wild and captive jaguars (*Panthera onca*). Masters Thesis, Columbia University, New York, NY.



## Media

### **MOTHERBOARD / VICE. 2018. “Living with Jaguars” virtual reality documentary**

Featured interview, technical advisor

*World Premiere at SXSW International Film Festival 2018, Austin, TX;*

*Featured in EarthX 2019, Dallas, TX;*

*Media coverage (Top 25 Favorites at SXSW, Magnetic Magazine);*

*Free 360 degree video on YouTube and full VR experience on Steam;*

*> 3 million views across all platforms*

<https://www.youtube.com/watch?v=1DdGPtSVncg>

[https://store.steampowered.com/app/874090/Living\\_with\\_Jaguars/](https://store.steampowered.com/app/874090/Living_with_Jaguars/)

<https://www.magneticmag.com/2018/03/sxsw-2018-film-preview/>

[https://motherboard.vice.com/en\\_us/article/zmg4ma/living-with-jaguars-vr](https://motherboard.vice.com/en_us/article/zmg4ma/living-with-jaguars-vr)

<https://www.panthera.org/livingwithjaguars>

### **Panthera Facebook Live. 18 December 2017. Alan Rabinowitz and Steve Winter Talk Jaguars**

Host

<https://www.facebook.com/pantheracats/videos/alan-rabinowitz-and-steve-winter-talk-jaguars/10155272151673763/>

<https://www.youtube.com/watch?v=jHAWe70UXMg>

### **National Geographic. 12 December 2017. “Jaguar versus Croc” documentary**

Technical advisor, credit: special thanks

*World premiere, NatGeoTV*

<https://www.usatoday.com/story/news/world/2017/12/12/jaguar-vs-crocodile-two-predators-fight-death/944197001/>

### **CBS 60 Minutes. 17 February 2013. “Update: In Search of the Jaguar”**

Content contributor, story; camera trap photographs of female F01 and cub

*Nationally aired, USA*

<http://www.panthera.org/60-minutes#watch>

### **Good News, RedeTV. 24 August 2012. “No Pantanal, a Equipe do Good News Segue o Rastro da Onça-Pintada”**

Interview

*Nationally aired, Brazil*

<http://www.youtube.com/watch?v=UfiDa9TfenU>

### **Globo Rural, Globo1. 25 November 2012. “Onça-Pintada é o Maior Felino Brasileiro”**

Interview

*Nationally aired, Brazil*

<http://globotv.globo.com/rede-globo/globo-rural/v/onca-pintada-e-o-maior-felino-brasileiro-e-atrai-turistas-no-pantanal/2258848/>

**National Geographic. 26 October 2011. “Hunt for the Shadow Cat”**

Technical advisor

*World premiere, NatGeoTV*

<http://channel.nationalgeographic.com/wild/big-cat-week/videos/hunt-for-the-shadow-cat/>

## **Presentations**

### **Drivers of jaguar (*Panthera onca*) distribution, density, and movement in the Brazilian Pantanal**

- Dissertation defense, SUNY ESF, Syracuse, NY 2019
- Pontifical Catholic University of Rio Grande do Sul, Porto Alegre, RS, Brazil 2019
- Panthera Conservation Science Meeting, Estes Park, CO 2019

### **Despots of the Wetland: density and behavior of an apex predator in disturbed landscapes**

- The Wildlife Society SUNY ESF Student Chapter Meeting, Syracuse, NY 2019
- Departmental lab meeting, SUNY ESF, Syracuse, NY 2018
- Invited Conservation Speaker, Niabi Zoo, Coal Valley, IL 2018
- Panthera Board meeting, Porto Jofre, MT, Brazil 2017
- Annual collaborator meeting, ICMBio/CENAP, Atibaia, SP, Brazil 2016
- Universidade Federal do Mato Grosso, Cuiabá, MT, Brazil 2016
- Projeto Onçafari, Miranda, MS, Brazil 2016

### **Spatially-explicit capture-recapture of jaguars (*Panthera onca*) in the Brazilian Pantanal**

- Departmental lab meeting, SUNY ESF, Syracuse, NY 2015
- The Wildlife Society NYS Chapter Annual Meeting, SUNY ESF Ranger School, Wanakena, NY 2015
- Annual collaborator meeting, ICMBio/CENAP, Atibaia, SP, Brazil 2013

### **Population persistence of jaguars (*Panthera onca*) in the Brazilian Pantanal**

- Applied Wildlife Science (EFB 491), SUNY ESF, Syracuse, NY 2012, 2013, 2014
- Local landowner meetings, Rancho Itapua, MdC; MS, MT, Brazil 2012, 2013, 2014
- Panthera Board meeting, Porto Jofre, MT, Brazil 2013
- Stanford University Study Abroad, Porto Jofre, MT, Brazil 2012
- Brazilian Marines Unit, RPPN Acurizal, MS, Brazil 2012
- The Wildlife Society Student Chapter, Cornell University, Ithaca, NY 2012
- Panthera Cat Advisory Council meeting, Porto Jofre, MT, Brazil 2011

### **Captive and wild jaguar (*Panthera onca*) hormones, genetics, and scat detection dog methodology**

- Principles of Genetics (EFB 307), SUNY ESF, Syracuse, NY 2014
- Intro to Conservation Biology (EFB 413), SUNY ESF, Syracuse, NY 2011
- WildCRU Panthers Program, University of Oxford, Oxford, UK 2008
- Association of Zoos and Aquariums (AZA) Annual Conference, Philadelphia, PA 2007

## Posters

**Devlin, A. L.**, P. G. Crawshaw, F. R. Tortato, and R. Hoogesteijn. 2012. A História da Pesquisa na RPPN Acurizal. RPPN Acurizal, Ecotrópica Foundation, MT, Brazil.

**Devlin, A. L.**, P. G. Crawshaw, and F. R. Tortato. 2012. A Pesquisa Atual na RPPN Acurizal. RPPN Acurizal, Ecotrópica Foundation, MT, Brazil.

**Devlin, A. L.**, P. G. Crawshaw, F. R. Tortato, and J. A. F. de Lima. 2012. Ecologia e Conservação da Onça-Pintada no Sítio Patrimônio Natural Mundial, Pantanal, Brasil. Pantanal National Park - Matogrossense, ICMBio, MT, Brazil.

**Devlin, A. L.** 2012. Population Persistence of Jaguars (*Panthera onca*) in the Brazilian Pantanal. NY State The Wildlife Society Annual Conference. Bronx Zoo, Bronx, NY.

Pomilla, C., B. J. Harmsen, R. J. Foster, **A. L. Devlin**, C. Bartholomew, C. H. Vynne, S. Carrillo-Percastegui, L. Maffei, J. Moreira, B. de Thoisy, and G. Amato. 2009. Large and fine scale genetic characterization of jaguars (*Panthera onca*) throughout their range. Society for Conservation Biology Annual Conference, Prague, Czech Republic.

## Awards and Funding (USD)

**Research Associate** 2016–present  
Source: Duncan and Ellen McFarland, Board members, Panthera, New York, NY  
Amount: \$300,000

*Preventing predation: experimenting with predator deterrent techniques in working cattle ranches*

**Kaplan Graduate Award** 2010–2014  
Source: Panthera, New York, NY  
Amount: \$54,510 total

*Dissertation: Despots of the Wetland: density and behavior of a solitary apex predator in disturbed landscapes*

**Project Donation** 2013–2014  
Source: Duncan and Ellen McFarland, Board members, Panthera, New York, NY  
Amount: \$2,500

*Pantanal Jaguar Project camera traps*

**Pack Travel Grant** 2014  
Source: SUNY ESF, Syracuse, NY  
Amount: \$400

*Spatial Capture-Recapture Workshop, Patuxent Wildlife Research Center / Cornell University, Ithaca, NY*

- Research Fellow** 2010  
 Source: Panthera Teton Cougar Project, Kelly, WY  
 Amount: \$5,000  
*Field training: kill site and GPS cluster searches; VHF radio-telemetry*
- Travel Award** 2008  
 Source: University of Oxford, Oxford, UK  
 Amount: \$2,500  
*Present to WildCRU Panthers; interview*
- Kaplan Graduate Award: extended funding** 2008  
 Source: Panthera / American Museum of Natural History, New York, NY  
 Amount: \$5,000  
*Masters thesis extension: Genetic structure of wild jaguars (*Panthera onca*) in Belize*
- Kaplan Graduate Award** 2007–2008  
 Source: Wildlife Conservation Society, New York, NY  
 Amount: \$25,000  
*Masters thesis: Fecal corticoid and reproductive hormone concentrations in wild and captive jaguars (*Panthera onca*)*

## Additional Professional Services and Skills

### Peer Reviewer

PLoS ONE; Biodiversity and Conservation; Mammalian Biology; Journal of Arid Environments

### Languages

English (native); Portuguese, Brazilian (spoken, written: proficient); Latin (written: 6 years); Spanish (spoken, written: novice)

### Certifications

Wilderness Survival (Cornell University, Ithaca, NY);  
 Certified Scat Detection Dog Handler (PackLeader Dog Training, Gig Harbor, WA);  
 Spatial Capture-Recapture Workshop (Patuxent / Cornell University, Ithaca, NY)

### Transportation

Automatic and manual automobile (NY state license); motorcycle (NY state license); boat pilot (NY state); ATV; horseback (24 years' experience)

### Interpersonal

Conflict resolution; team leadership; active team member; field training of team members and volunteers; consistent interaction with local communities, governmental agencies, and non-governmental organizations