CIDADE MEGADIVERSAS: COMO E POR QUE ANIMAIS AMEAÇADOS PERSISTEM EM GRANDES CENTROS URBANOS

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1. Introdução

A exploração humana dos ecossistemas tem alterado drasticamente os ambientes naturais, resultando em declínios populacionais e perda de espécies em âmbito global (Pimm e Raven 2000). As taxas atuais de extinção de espécies são tão elevadas que alguns autores têm considerado que vivemos um novo período de extinção em massa, comparável às grandes extinções que ocorreram no passado geológico (Pimm et al. 1995, Dirzo e Raven 2003). As projeções futuras são alarmantes e indicam a perda de até 50% das espécies nos próximos 100 anos (Brook et al. 2003).

Embora existam diversos fatores que contribuem para essa alta taxa de extinções introdução de espécies exóticas, erosão genética, aumento da ocorrência de doenças, pressão de caça), a perda e a fragmentação dos habitats permanecem como os principais responsáveis pela crise da biodiversidade (Fahrig 2002). A maioria dos ecossistemas mundiais está modificada em tal magnitude que será impossível trazê-los ao estado original (Hobbs et al. 2006). Por isso, devemos estar preparados para reconhecer e manejar ecossistemas profundamente alterados pelas atividades humanas, como aqueles encontrados em pequenos e grandes centros urbanos (Hobbs e Harris 2001, Hobbs et al. 2006, Davis et al. 2011).

A ferramenta largamente usada nas últimas três décadas para conservar espécies animais foi a intensificação da criação de áreas protegidas, normalmente extensas áreas públicas com habitat íntegro (Sánchez-Azofeifa et al. 1999). No entanto, pesquisadores tem reconhecido que a conservação efetiva da biodiversidade só será garantida em longo prazo quando incluirmos as áreas privadas e centros urbanos na agenda conservacionista, realizando intervenções proativas que impeçam e revertam os processos de extinção (Norton 2000, Theobald e Hobbs 2002, Seddon et al. 2007).

Movimentar-se é a característica mais conspícua que animais realizam para acessar suas necessidades básicas de sobrevivência, alimentação e reprodução, e assim persistir em determinado local (Nathan 2008, Nathan et al. 2008). O processo de urbanização é talvez o tipo mais agressivo de perda e fragmentação de habitat. As paisagens resultantes deste processo sofrem intensa conversão de vegetação nativa em estruturas não naturais e os remanescentes de áreas naturais são pequenos, esparsos e isolados por estruturas urbanas que impedem a movimentação, e por consequência a sobrevivência dos animais.

A urbanização cria um habitat inteiramente novo – a cidade, onde espécies nativas precisam aprender como se deslocar para usar esse ambiente e persistir em longo prazo. Obviamente, centros urbanos são sempre muito mais pobres em espécies que seu entorno rural ou conservado (Schochat et al. 2004, Bradley et al. 2008, Grimm et al. 2008), pois apresentam recursos vegetais extremamente pobres e impõe estruturas físicas (e.g edificações e ruas) que dificilmente podem ser atravessadas pelos animais.Por isso, muitas espécies, principalmente aquelas grandes, são as primeiras a se extinguir nestas áreas (Schochat et al. 2004).

Apesar dessa grande perda de espécies, diversos estudos tem demonstrado a importância da quantidade e da disposição das estruturas vegetais e urbanas na persistência de grandes vertebrados dentro de cidades (Blum 2008). Curiosamente, alguns centros urbanos tropicais (e.g. cidades sul-mato-grossenses) conseguem manter populações de grandes vertebrados, enquanto outros se tornam grandes desertos estéreis em termos de biodiversidade.

O desafio de conservação da fauna nesse cenário urbano está lançado, pois se faz necessário entender como e por que algumas espécies de vertebrados com forte interesse de conservação conseguem persistir em alguns centros urbanos e em outros não. É preciso entender como esses animais se deslocam nas cidades usando e evitando certas estruturas naturais e urbanas para acessar locais de alimentação, descanso e reprodução. Esse conhecimento nos habilitará a planejar cidades que contemplem com mais eficiência a conservação de espécies da fauna nativa

2. Objetivos Gerais

Inferir, através do monitoramento remoto do movimento de indivíduos, como e por que algumas espécies de animais silvestres conseguem persistir em grandes centros urbanos, visando identificar estruturas naturais e urbanas responsáveis pela atração ou repulsão dos indivíduos. A partir essas informações pretendemos subsidiar cientificamente planos diretores municipais, programas de ordenação viária e de arborização que favoreçam o aumento e a manutenção da biodiversidade em grandes centros urbanos.

3. Objetivos Específicos

(1) Monitorar o movimento de três espécies de animais com características de deslocamento e movimento distintas (a capivara Hydrochoerus hydrochaeris, o gambá-de-orelha-branca *Didelphis albiventris* e o cágado-de-barbicha *Phrynops geoffroanus*) no ambiente urbano de Campo Grande-MS;

(2) Identificar e estimar as áreas de vida dos indivíduos, os horários de movimentação e uso de habitat das espécies estudadas;

(3) Identificar os diferentes estados comportamentais (forrageio, descanso e rotas de deslocamento) realizados pelas espécies nas diferentes áreas de movimentação;

(4) Identificar estruturas chaves onde são realizados os diferentes estados comportamentais (forrageio, descanso e deslocamento) pelas espécies estudadas;

(5) Identificar quais estruturas naturais, urbanas e/ou viárias atraem e/ou repelem as espécies nos seus processos de movimentação;

4. Métodos

4.1. Áreas de estudo e Unidades de Conservação Previstas

Inicialmente foram previstas 3 Unidades de Conservação como áreas de estudos, eram elas: Parque das Nações Indígenas, Parque Estadual do Prosa e Parque Estadual Matas do Segredo, no município de Campo Grande/MS. No entanto, no decorrer da pesquisa, por questões logísticas e financeiras, optamos por concentrar as atividades somente no Parque das Nações Indígenas (Figura 1, PNI) (20.452°N, 54.572°O).

O PNI é o maior parque urbano da cidade, contando com uma extensão de 119 ha. É caracterizado por uma vasta área aberta coberta por gramíneas e uma área florestal linear com cerca de 6 ha no meio do parque. Dentro desta área florestal há um córrego de aproximadamente um quilômetro que conecta uma represa, com cerca de 0,39 ha, e um lago artificial de aproximadamente 4,68 ha.

4.2. Espécies alvo

Inicialmente o projeto proposto envolvia o estudo da movimentação em ambiente urbano de três espécies, no entanto devido a diversas dificuldades de ordem logística, principalmente, a execução dos objetivos relacionados aos gambás-de-orelha-branca não foram realizados. Os cágados-de-barbicha *Phrynops geoffroanus* foram estudados por nossa equipe de pesquisa na região do Lago do Amor na Universidade Federal de Mato Grosso do Sul. Por se tratar de uma área de estudo fora de Unidades de Conservação Estaduais, as informações referentes a esta pesquisa não serão apresentadas neste relatório.

Esta pesquisa foi devidamente autorizada pelos órgãos competentes: SISBIO 49802-2, 49802-3, 49802-4, 49802-5 e 49802-6; CEUAUFMS 676/2015 e 1.046/2019.

4.3. *Captura e movitoramento de capivaras*

As capivaras foram capturadas por contenção química composta por uma solução anestésica de Tiletamina (dose: 2mg/kg) e Zolazepan (dose: 2mg/kg) (Zoletil ®VIBRAC). O critério de seleção desses animais se deu pela escolha daqueles que estivessem à uma distância segura de corpos d'água, locais com alto risco de afogamento durante a indução anestésica. A administração dessa solução foi feita por via intramuscular através do lançamento de um dardo efetuado por um rifle (MODEL J.M.DB13 ®DANINJECT) após a aproximação de um observador a pé (5-10 metros). Após a indução anestésica, os indivíduos foram sexados, pesados, marcados com brincos coloridos numerados e com colares de rastreamento contendo um GPS (Colar GPS ®TIGRINUS). Durante esse processo, um médico veterinário acompanhou em intervalos de dez minutos os parâmetros vitais dos indivíduos: frequência cardíaca, frequência respiratória, temperatura retal, tônus muscular, reflexo auricular, ocular e do esfíncter anal e também checaram a presença de ectoparasitas, ferimentos e outros sinais de comprometimento à saúde dos animais. Esse acompanhamento visou assegurar o bem-estar dos indivíduos, e indicar se alguma intervenção médica adicional seria necessária. Cada colar GPS foi programado para gravar a localização geográfica dos indivíduos a cada 30 minutos, bem como a data e a hora dos registros. Uma vez a cada mês, os colares ficaram disponíveis para enviar os dados gravados, remotamente. Por isso, em regime mensal, as localizações foram transmitidas a um receptor UHF (Receptor ®TIGRINUS).

As capturas e o monitoramento dos indivíduos foram realizadas em três períodos de amostragem entre os anos de 2018 e 2022. Em cada período um indivíduo de cada grupo social foi capturado e equipado com colar-GPS.

5. **Resultados**

Foram capturados 18 indivíduos de capivara *Hydrochoerus hydrochaeris,* pertencentes a seis grupos sociais residentes no PNI (Tabela 1). Suas áreas de vida variam entre 14,9 e 47,6 ha, havendo pouca sobreposição entre os grupos sociais, com limites bem claros definindo a movimentação das diferentes famílias (Figura 1). Resultados detalhados referentes aos objetivos 3, 4 e 5 estão amplamente apresentados e discutidos nas produções científicas provenientes desta pesquisa e entregues anexas a este relatório.

2018 — 2022

Tabela 1. Capivaras *Hydrochoerus hydrochaeris* capturadas no Parque das Nações Indígenas, Campo Grande/MS, durante a vigência da pesquisa.

Indivíduo	Sexo	Peso (Kg)	Desfecho
La39La21	M	55	colar retirado
Br23Br22	F	54	colar retirado
Br24Br25	F	50	colar retirado
La18La19	M	48	colar retirado
Am01Am02	F	58	colar retirado
Vd23Vd24	F	44	colar retirado
La16La17	M	61	colar retirado
Am32Vd25	M	57	colar retirado
Az11Az12	F	59	colar retirado
Vd06Vd07	M	55	colar retirado
Br40Br39	F	54	colar retirado
Az10Br03	M	56	colar retirado
Ve17Ve16	M	68	colar no animal
Vd21La20	F	62	colar no animal
Ve22Ve23	F	56	colar no animal
Am03Am04	F	68	colar no animal
Az22Az23	M	58	colar no animal
Br27Br26	F	58	colar no animal

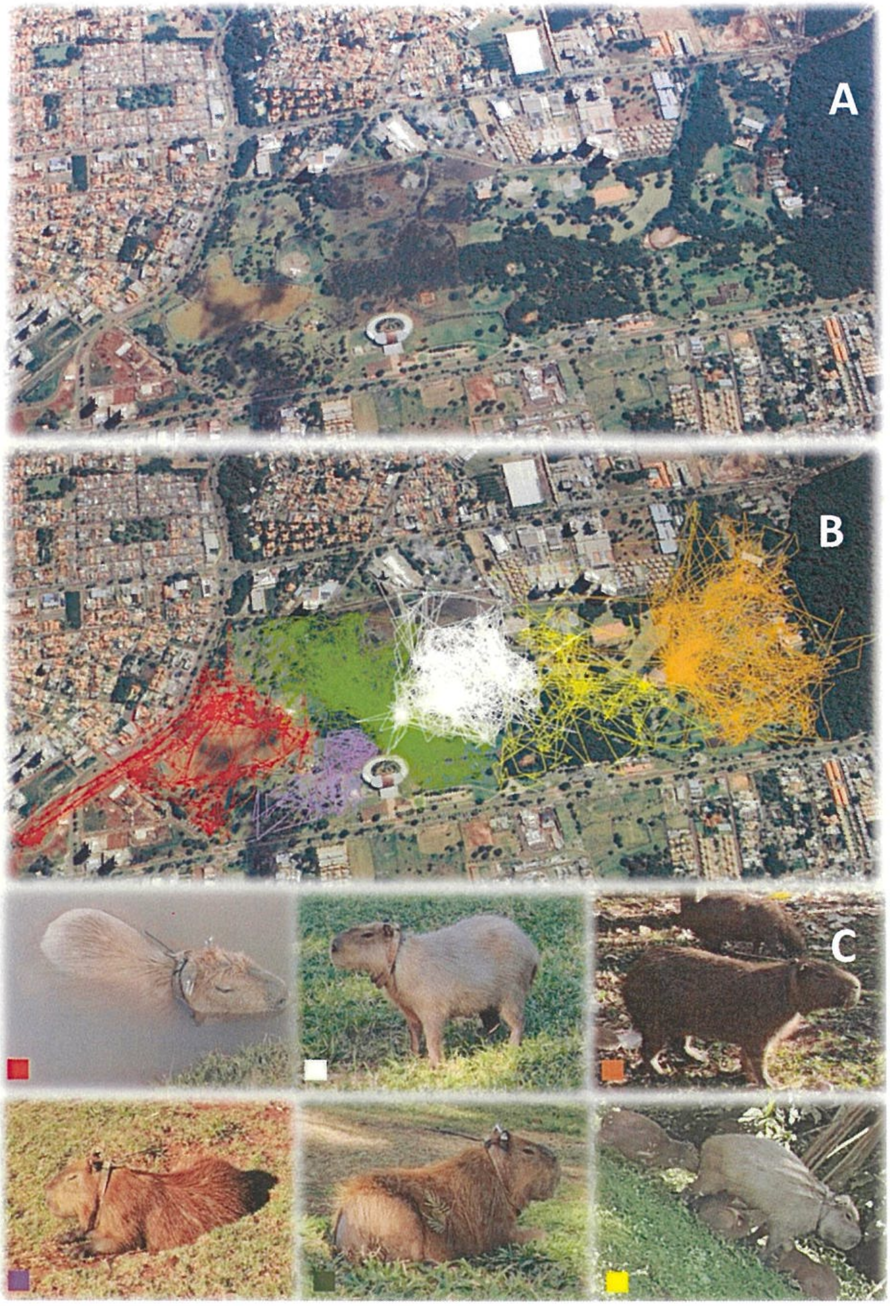


Figura 1. (A) Área do Parque das Nações Indígenas (PNI), Campo Grande/MS. (B) Áreas de vida dos grupos sociais de capivara *Hydrochoerus hydrochaeris* monitorados no PNI. (C) Indivíduos equipados com colares-GPS.

6. **Produção Científica**

Resumos

- Resumo apresentado pela estudante de Iniciação Científica Renata Dias no X Seminário de Pesquisa e Encontro de Iniciação Científica do ICMBio entre 17 e 20 de setembro de 2018 intitulado "Área de vida e uso de habitat de capivaras em centros urbanos".

Dissertações

- Dissertação de mestrado defendida em maio de 2018 pela estudante Samara Serra Medeiros na Pós-graduação em Ecologia e Conservação/UFMS intitulada "Área de vida, seleção de habitat e atividade diária de capivaras vivendo em uma área urbana".

- Dissertação de mestrado defendida em maio de 2020 pela estudante Ana Carolina França Balbino da Silva na Pós-graduação em Ecologia e Conservação/UFMS intitulada "Identificação de variáveis urbanas que determinam a probabilidade de atropelamento de *Hydrochoerus hydrochaeris* (Linnaeus, 1766) em um ambiente urbano".

Artigos científicos

Serra-Medeiros S., Ortega Z., Antunes P.C., Herrera H.M., Oliveira-Santos L.G.R. 2021. Space use and activity of capybaras in an urban area. Journal of Mammalogy, 102(3):814–825.

Balbino-Silva A.C.F., Menezes J.F.S., Oliveira-Santos L.G.R. 2022. Roadkill risk for capybaras in an urban environment. Landscape and Urban Planning 222 (2022) 104398.

7. **Referências Biblioráficas**

Blum, A. The Long View: Urban Remediation through Landscape and Architecture. 2008. Metropolis Magazine 10:92-95. Bradley, C. A., S. E. J. Gibbs, e S. Altizer. 2008. Urban land use predicts West Nile Virus exposure in songbirds. Ecological Applications 18:1083-1092.

Brook, B. W., N. S. Sodhi, e P. K. L. Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424:420-426.

Davis, M. A, M. K. Chew, R. J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. a Pickett, J. C. Stromberg, P.

Del Tredici, K. N. Suding, J. G. Ehrenfeld, J. P. Grime, J. Mascaro, e J. C. Briggs. 2011. Don't judge species on their origins. Nature 474:153-154.

Dirzo, R., e P. H. Raven. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137–167.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold : a synthesis. Ecological Applications 12:346–353.

Grimm, N. B., S. H. Faeth, N. E. Golubiewski, C.L. Redman, J. Wu., X. Bai, e J. M. Briggs. 2008. Global changeand ecology of cities. Science 319:756-760.

Hobbs, R. J., e J. A. Harris. 2001. Restoration Ecology: Repairing the Earth's Ecosystems in the New Millennium. Restoration Ecology 9:239–246.

Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, V. A. Cramer, P. R. Epstein, J. J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, e D. M. Richardson. 2006. Novel ecosystems : theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Nathan, R. 2008. An emerging movement ecology paradigm. PNAS 105:19050–19051.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, e P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. PNAS 105:19052–19059.

Norton, D. A. 2000. Conservation biology and private land: shifting the focus. Conservation Biology 14:1221–1223.

Pimm, S. L., e P. Raven. 2000. Extinction by numbers. Nature 403:843–845.

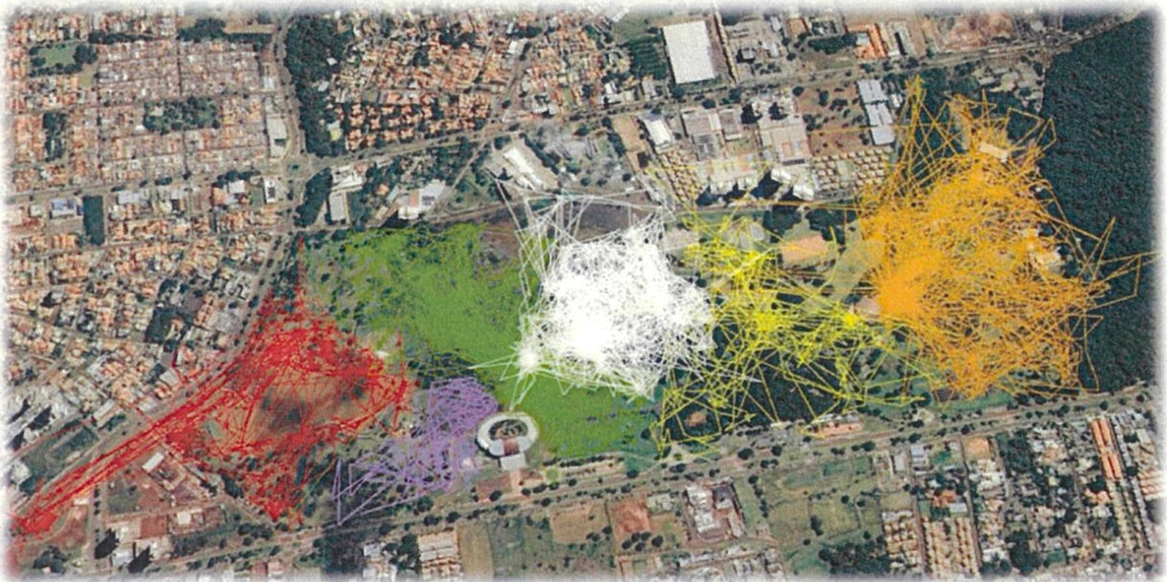
Pimm, S. L., G. J. Russell, J. L. Gittleman, e T. M. Brooks. 1995. The Future of Biodiversity. Science 269:347–350.

Sánchez-Azofeifa, G. A., C. Quesada-Mateo, P. Gonzalez-Quesada, S. Dayanandan, e K. S. Bawa. 1999. Protected areas and conservation of biodiversity in the tropics. Conservation Biology 13:407–411.

Schochat, E., W.L. Stefanov, M.E.A. Whitehouse, e S.H. Faeth. 2004. Urbanization and spider diversity: influences of human modification of habitat structure and productivity. Ecological Applications 14:268-280.

Seddon, P. J., D. P. Armstrong, e R. F. Maloney. 2007. Developing the science of reintroduction biology.Conservation Biology 21:303–312.

Theobald, D. M., e N. T. Hobbs. 2002. A framework for evaluating land use planning alternatives : protecting biodiversity on private land. Conservation Ecology 6:5.



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Research Paper

Roadkill risk for capybaras in an urban environment

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HIGHLIGHTS

- We developed a new method to estimate roadkill hotspots in cities.
- Capybara roadkill hotspots occurred near parks and water bodies.
- Distance to parks was the main predictor of capybara roadkill.
- Mitigation actions next to parks could decrease roadkills.

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ABSTRACT

Wildlife vehicle-collision is one of the most visible negative effects that roads exerts on animals and has increased dramatically across the world. Despite its conspicuousness, studies about roadkills in cities have been neglected lacking in road ecology. We developed new approach for estimating capybara roadkill hotspots in Campo Grande, a big city in Brazil. We also investigated potential driving factors correlated with roadkill occurrence, to build a predictive roadkill map for the entire city and propose mitigation measures. We monitored capybara roadkills for thirteen years and found hotspots using a graph-based kernel density estimation. We tested four predictors to identify which characteristics influence roadkill occurrence: distance from water bodies, distance from parks, vegetation cover, and traffic flow. We used a generalized linear mixed model to test for significant effects and to predict roadkill occurrences. Hotspots analysis showed four hotspots surrounding large green areas and water bodies, probably due to capybara habitat and physiological requirements. The predictive map shows latent hotspots, locations that have the characteristics necessary for a capybara to live but where we do not have observed deaths. To mitigate risk, we recommend using speed reduction tools around parks. A decrease in capybaras roadkills could positively impact human population welfare and material damage caused by these collisions.

1. Introduction

Rapid human population growth and urbanization increase the building of linear infrastructures (e.g. streets, roads and rails), which can isolate wildlife populations and, in turn, reduce local genetic diversity ( ). Even when linear structures are not full barriers to movement, they may still be responsible for significant negative impacts, changing animal movement and behavior ( ). Road kills have been considered the most visible negative direct effect of linear infrastructures on wildlife ( ).

Beyond the negative effects exerted on wildlife populations, roadkills can also cause physical and psychological injuries to humans, as well as material and economic costs to society ( ). Roadkills numbers have increased dramatically across the world, numbering in the millions per year in some countries ( ). These numbers are just the tip of the iceberg, an underestimation due to the lack of reports and destruction of carcasses ( ).

Urban fauna brings both negative and positive aspects to cities. They increase the likelihood of human-wildlife conflicts, as damage to agricultural fields and gardens ( ), as well as transmission

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of zoonotic diseases ([illegible]). On the other hand, wildlife can provide unique ecosystems services withing cities including increase in psychological wellness for humans ([illegible]). Nevertheless, urban wildlife is relatively unexplored when compared to wildlife in natural environments ([illegible]), even though cities hold half of the world's human population ([illegible]). Therefore, it is necessary to bring road ecology and conservation planning to cities, so that urban plans can include wildlife as its component. With that, cities can pursue an acceptable degree of environmental sustainability ([illegible]).

A common conservation planning tool that might be useful in our study is a hotspot analysis ([illegible]). Hotspots are a statistical or analytical set of approaches that seek to identify greatest or statistically significant locations in space. In this case, hotspot analysis can be used to detect places where vehicle collisions with fauna are disproportionally more frequent when compared to other places ([illegible]). They are usually correlated with certain habitat and landscape features ([illegible]). Thus, mapping and modeling those would allow researchers to forecast current and potential areas of conflict, as well as the extrapolating when planning further roads ([illegible]). Knowledge of which areas are more likely to have conflict can have help planners implement mitigation measures.

Capybaras are excellent models for the study of roadkills. They are common in urban landscapes composed of managed grasslands and lakes, due to the lack of predators, and a high and stable availability of resources patches ([illegible]). In urban environments where they occur, capybara populations can be higher than in natural ones, which makes it one of the species involved in vehicle collision ([illegible]). As a result of this abundance, this species is an excellent object of study: it provides ample opportunity for sampling and is one of the species most involved in the number of accidents.

In this study we aimed to reveal roadkill hotspots within a big tropical city and investigated potential driving factors linked to roadkill risk of a large, nocturnal, social mammal (capybaras *Hydrochaeris hydrochaeris*; [illegible] b). We plotted the roadkills in a map of the city in a way that it is possible to visualize the roadkill aggregations. After that, we tested four environmental predictors that are usually correlated with road kills ([illegible]): the effect of vegetation cover, distance to water bodies, distance to parks, and traffic flow. If at least one of these variables is significant, we can build predictive roadkill risk map for the entire city with them. We expected distance to parks to be the variable that most influenced capybaras roadkill as it should explain fairly well the abundance of those animals.

2. Methods

2.1. Study site and data collection

We carried out this study in the urban area of Campo Grande city, Mato Grosso do Sul, Brazil (−20.469° N, −54.620° W; [illegible] A). Currently, Campo Grande has a human population of ca. 875,000 people ([illegible]) and urban area of ca. 36,000 ha, presenting ca. 4,000 km of roads, of which 71% are paved roads, organized in a reticulate street network. Campo Grande is located mostly within the hydrographic basin of the Paraná river, with 28 water springs and 11 watersheds bypassing the urban area, most of them bordered by grassland and forest. Remaining forest vegetation represents 21% of the city area, and it is mostly located inside urban parks. In places like this, the presence of food resources, shelter, conspecifics, and lack of predators allows the existence of a diverse wild vertebrate fauna, including capybaras ([illegible]). In Campo Grande city, several large groups of capybaras live inside partially fenced parks, while often walking through the city. Meanwhile, other smaller groups live in the middle of the city, composed of a cluster of buildings that does not allow animals to walk among them, only through the streets under greater risk of being run over.

Roadkill monitoring occurred through five methods: (1) A partnership with Solurb, the waste disposal company responsible for gathering dead animals from the roads, where they would report collection of carcasses; (2) by the Quapivara App, developed by the State Public Prosecutor's Office, in which the citizens could send a text message, informing the roadkill occurrences with pictures to confirm species identification; (3) by going through historical media coverage on capybara roadkills; (4) through opportunistic sightings made by the authors; (5) by contacting the local wildlife rehabilitation centers, which received injured animals collected by the environmental police. For each roadkill occurrence we registered the street, date and geographic coordinates and checked for duplicate information and removed when it was necessary. To calculate the hotspots, we used a network-based kernel density estimation (NKDE).

2.2. Determining hotspots

In this study, we have a reticulated network structure, a mesh of roads from a city. Due to that, two-dimensional that ignore this mesh structure would be unrealistic, since animals are essentially constrained

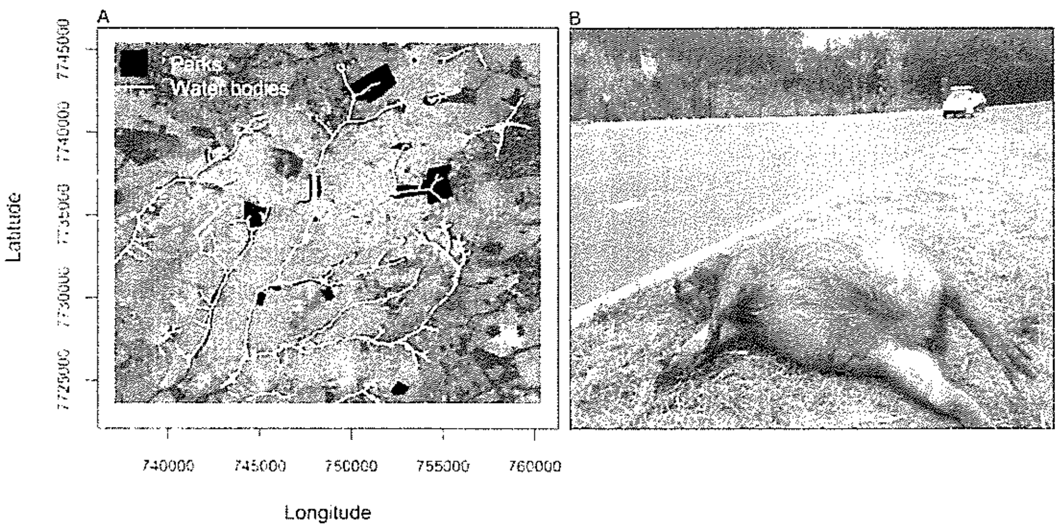

Fig. 1. Map of Campo Grande city with highlighted rivers (A) and a picture of a capybara killed in a road accident (B).

to move through roads while the method would not be. We started by acquiring road infrastructure maps from 2019 available in the website of the city council (with projection UTM and datum WGS84; available at: [illegible]). After that, we converted this road map to a graph ([illegible]), by considering every road intersection as a vertex, and every street as an edge. We then matched each roadkill to its nearest vertex, and assigned to each vertex a value equal to the number of roadkills associated to it. From there, we assigned a value to every other vertex, based on their distance to the roadkill vertices. This value was given by the Gaussian kernel formula:

$$V(x) = \frac{1}{nh}\sum_{i=1}^{n}\frac{1}{\sqrt{2\pi}}e^{-0.5x_i^2/h^2}$$

Where x is the shortest graph distance between this vertex and the roadkill vertexi. This value was divided by the bandwidthh^2, a parameter that decreases the importance of distance in reducing the chance of an occurrence. In other words, larger bandwidth extends the area of the hotspot, and a smaller bandwidth decreases it. We used $h = 310$ meters, because this value is equivalent to the radius of a capybara home range in the city ([illegible]). This method is equivalent to other implementations of network kernels ([illegible]). We used the 95% and 50% isopleth of probability of the roadkill in all streets and assigning values of roadkill probability to each section.

To identify which environmental characteristics increase the odds of a roadkill event, we used four environmental predictors that are usually correlated with road kills ([illegible]): distance from the nearest water bodies, distance from the nearest park, vegetation cover, and traffic flow. These are factors correlated with capybaras habitat use (and consequently with capybara, high abundance; Medeiros et al., accepted in Journal of Mammalogy) and with traffic flow, factors usually correlated with mammals' roadkill ([illegible]). We used the Normalized Difference Vegetation Index. (NDVI) from June 2019, to describe the variation of greenness of the vegetation ([illegible]). The NDVI data were obtained using the LANDSAT 8 images acquired from Earth Explorer ([illegible]) with 30 m resolution. The NDVI has a direct relation with aboveground net primary productivity, and has been used as a predictor of biological patterns for vertebrates, including species richness, abundance, distribution, and landscape connectivity ([illegible]). We defined a buffer with radius of 100 m, ([illegible]) around each roadkill point and retrieved the median of the NDVI. Traffic flow was measured using distance to the city's centroid as a proxy. The distance to water bodies and parks were made using the same infrastructure map that was used for estimating the hotspots. Distances were calculated following the shortest path through the streets, using the package stplanr ([illegible]) in R ([illegible])). With that, we could estimate all variables for all roadkill occurrences.

To create a comparison, we created 100 random points for every roadkill as pseudo-absence points, where no roadkill has been registered. The four variables were measured for each pseudo-absence point. Comparing presence to pseudo-absences allows us to identify if a characteristic increases the odds of a roadkill, but this estimation might be biased by spatial autocorrelation. It is possible that two roadkill events were related to one another if close enough, and thus cannot be considered independent samples. To find out if that was the case, we tested the presence of autocorrelation using Moran I test using the five nearest neighbors. We detected evidence of autocorrelation ($I = 0.251$; $p = 0.0057$), and thus used a model that considers this autocorrelation explicitly. We also used Pearson's autocorrelation test between parks within water bodies and parks within green areas. In both cases, the autocorrelation was low ($r^2 = 0.144$; p= <2.2e-16, $r^2 = 0.007$; p = p < 2.2e-16, respectively).

To determinate which factor would increase the chances of a roadkill, we used a Generalized Linear Mixed Model, with penalized quasi likelihood (glmmPQL; [illegible]). This method is a modification of general linear models, in which one can specify the correlation between samples. For each sample, we calculated a different correlation matrix, with the five nearest samples. In this correlation matrix, distance between the focal point and its neighbors decreased the correlation by a negative exponential function. Doing so allowed us to control for the previously detected autocorrelation. We used a binary variable (0 = randomly selected points and 1 = roadkill occurrences) as a response variable. The four explanatory variables above cited were used as explanatory variables. To test if the variables are correlated, we test collinearity between them and it was low (ndvi = 1.362; water = 1.377; park = 1.360; centroide = 1.157).

2.3. Predictive roadkill map

To determinate the intensity of events of a roadkill that could happen in each street (graph edge), we made the predictive roadkill capybara map using glmmPQL results. For a better visualization of the areas with high predicted risk of roadkill, we identified the streets that held 50% and 95% of the overall probability. For checking the predictive performance of our model, we reran our glmmPQL using 70% of our data, and used the remaining 30% to calculate the average Area Under the Curve (AUC). This process was repeated 1000 times to ensure there are no biases in selecting this subset. We reported the average AUC as a measure of accuracy.

3. Results

We recorded 125 roadkill events between 2006 and 2019 ([illegible] A). Most of them (70%) were taken in 2019 due to the agreement signed between researchers and public administration to record, monitor and plan actions to reduce roadkills. Hotspots analysis revealed four complexes of hotspots within the city ([illegible] B), mostly around parks, large green areas and water bodies.

Capybara roadkill probability was negatively affected by distance to parks ($\beta = -0.0017$; $z = -0.0017$; $df = 12496$; $p < 0.001$) and water bodies ($\beta = -0.0017$; $z = -0.0017$; $df = 12496$, $p < 0.001$), and positively affected by forest cover ($\beta = 5.3$; $z = 2.04$; $df = 12496$; $p < 0.01$) and traffic flow ($\beta = 0.00023$; $z = -0.00004$; $df = 12496$; $p < 0.01$) ([illegible] A, B). Assuming an exponential decaying, the control of spatial autocorrelation structure indicated a variogram with range = 0.94 and nugget = 4×10^{-10}. Standardized coefficients pointed out distance to parks as the main driver of roadkill risk ($\beta = -1.50$; $z = -5.331$; $df = 12624$), followed of distance to water ($\beta = -0.80$; $z = -3.87$; $df = 12624$; $p < 0.01$) traffic flow ($\beta = -0.64$; $z = -5.14$; $p < 0.01$; $df = 12624$) and forest cover ($\beta = 0.26$; $z = 3.049$; $p < 0.01$; $df = 12624$). This model presented a predictive capacity of AUC = 0.60, with a confidence interval between 50 and 70), mainly due to the high rate of commission error. On the other hand, the rate of omission error, i.e. do not predict areas of risk those with lots observed roadkills, was extremely low ([illegible] A, D).

4. Discussion

Road kills concentrated mostly around the parks, probably reflecting capybara abundance in those areas ([illegible]). Some studies found that roadkill numbers are higher within parks than out of them due the higher abundance of animals ([illegible]). Likewise, previous studies already pointed out that capybaras mortality patterns were related to the proximity to river and vegetation ([illegible]), characteristics found inside parks and contribute for high abundance of capybaras. Those factors could explain

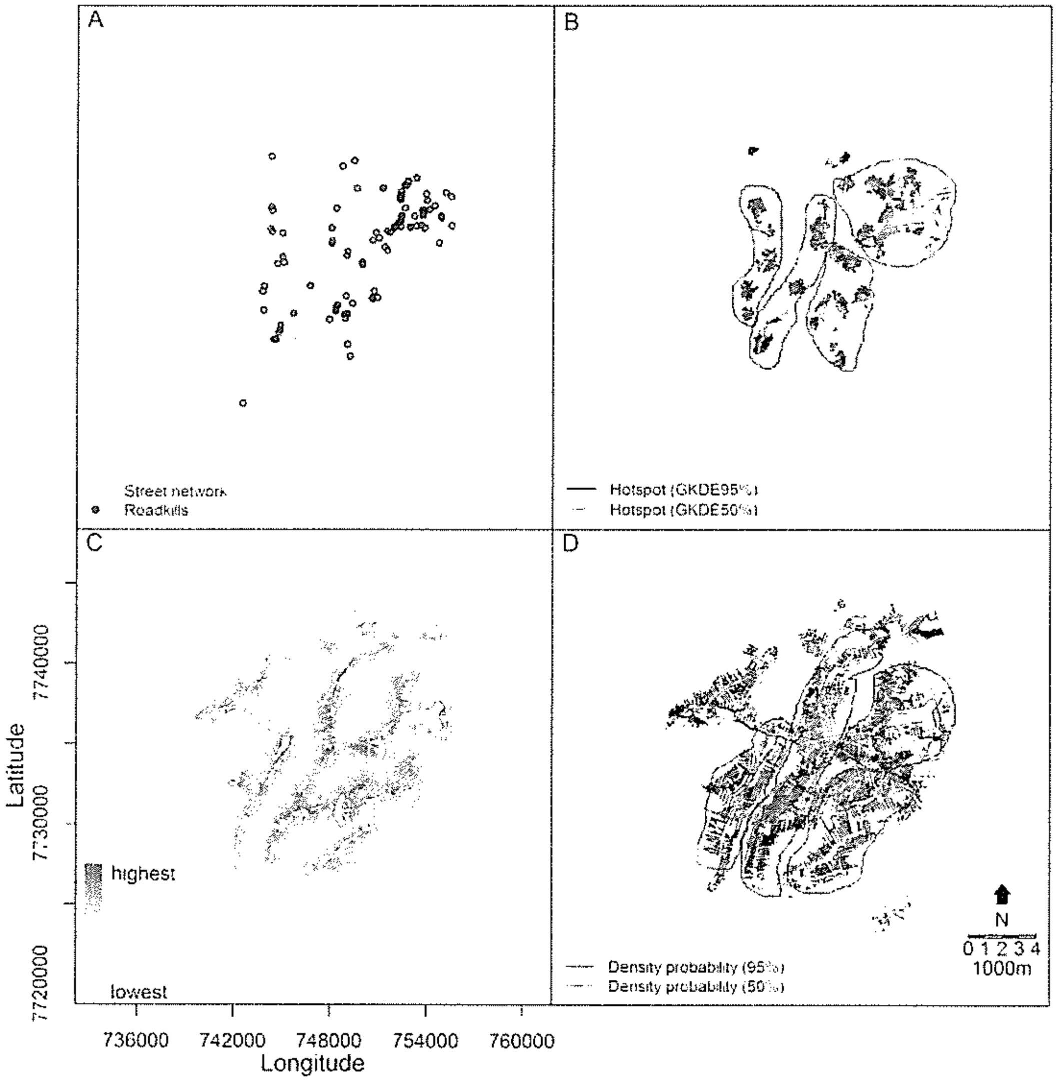

Fig. 2. Spatial distribution of capybara road kills, with hotspots at Campo Grande city's streets. The circles represent the hotspot complexes. The grey lines are the street system network, with the black lines representing the hotspots with 95% density probability and the red line representing the hotspots with 50% density probability. A) A map of roadkills locations along urban area of the city, represented by red points; B) Actual hotspots, represented with 50% e 95% confidence intervals; C) Predictive map of roadkills, represented as the probability of a roadkill. D) Hotspots based on the predictive roadkill map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

why distance to parks was the variable that most influenced capybara roadkill in our study.

The four hotspots were concentrated in places with a combination of water bodies and high vegetation cover, which have been indicated for capybaras along roads ([illegible]). The significant increase in roadkill odds with proximity to water and vegetation cover also indicates these two factors are dominant factors in road killings, and the preference of capybara for these habitats ([illegible]). These findings further reinforce the hypothesis that the main characteristics necessary for capybaras roadkills is the presence of suitable ([illegible]).

Traffic flow has been identified as the most influential variable for mammals roadkill in several studies ([illegible]). We did not find that in our study, where it was the third most important variable, possible because the network of streets in cities works as a barrier for capybara crossing. In other words, capybara would avoid high traffic flow roads, thus reducing the chances to be hit, as it is well documented for other species too ([illegible]). Another explanation for the reduced effect of traffic is related to animal activity. Capybaras graze in groups ([illegible]) and are more active at night ([illegible]). Both these characteristics can increase roadkill chances ([illegible]). But in cities, traffic flow is lower at night ([illegible]) and the reticulated system could impede high velocity as in highways. Those factors, alone or together, can explain why traffic flow was less influent in our study.

The predictive map showed the presence of hotspots forming near water bodies, similar to the hotspot analysis done on the original roadkill data. However, the predicted analysis also revealed hotspots that were shown with the original roadkill data. One possible explanation for predicted but unrealized hotspots is that animals in these areas are living mostly inside fenced parks, and cannotn easily go outside, controlling roadkill. Some of those points could be also a commission error, that is, a false positive. Since, we modeled only one variable related with driver behavior (i.e. traffic flow), it is possible that our predictor is reflecting solely the chance of finding capybaras in the region. Thus, these predictions could not be a false positive but a reflection of how suitable this environment is for capybaras. Although it would be better to avoid false positives, one can argue this type of error is the least concerning for conservation. One could argue that it is better to identify non-existing hotspots and waste some effort, than to miss an existing

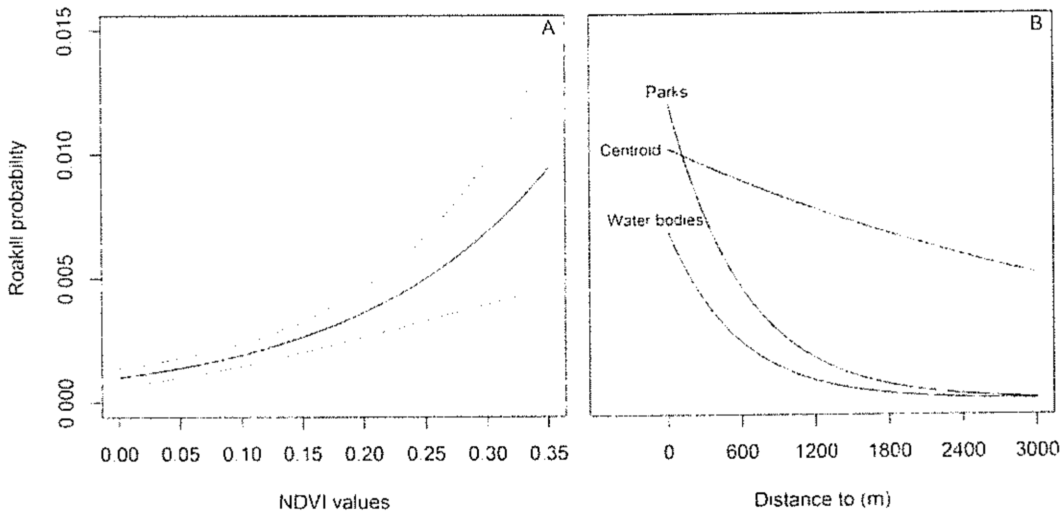

Fig. 3. GLM results of capybaras roadkill probability, with the variables in x axes and roadkill probability in y axes. Solid lines represent probability values, dashed lines represent 95% confidence intervals. In B, standardized errors for water bodies, centroid and parks, are respectively: 0.0004, 0.0003 and 0.00004 m.

hotspot and suffer from a greater number of accidents. Hotspot areas without accidents are still areas that the animals can access and move to new places to establish and forms new groups ([illegible]). Because of that, we suggest considering all hotspots in planning mitigation actions.

For reducing wildlife vehicle collisions, many transport agencies are trying different methods. They are divided in those that modify animal behavior and those that modify user behavior. Regarding changes in animal behavior, the combination of fence walls and safe passages might be the best mitigation actions ([illegible]) and the costs analyses clearly support the installation of these devices ([illegible]). Other methods include olfactory repellents sprayed on vegetation and structures along the road, ultrasound and road lighting ([illegible]). Meanwhile, in an urban environment, those methods can be not easily to be installed due to the environmental characteristics (e.g. flat topology, absence of appropriate areas for wildlife passages, and difficult imposed to pedestrians).

In an urban environment, we recommend the modification of user behavior. Wildlife collision is often associated with high speed ([illegible]), so the installation of warning signals, speed bumps, reducing speed limit, and increasing enforcement of current speed limits, could be effective in reducing the number of roadkills ([illegible]). If the city managers decide to use warning signs, we recommend using them concomitantly with other mitigation structures, because they show little effect when done alone ([illegible]). One approach would be installed next to the culverts, because the animals can use this infrastructure as a corridor between patches and to avoid vehicles ([illegible]). Installing mitigation measures close to rivers and green areas could also be suitable for multi-species conservation approach. Other species found in Campo Grande city, such as coati (*Nasua nasua)*, crab eating fox (*Cerdocyon thous*), and giant anteater *(Myrmecophaga tridactyla)* that live within urban parks, and could also benefit from greater speed reduction next to green areas.

We also recommend decreasing the traffic flow in those areas. Surrounding the two biggest hotspots are recreation areas, often open at night. These areas could increase the probability of roadkill accidents since they show greater traffic flow when capybaras are most active. So, we recommend advising the population to look for alternative routes, parking a couple blocks away from these centers, and using the public transport system. We also recommend increasing the enforcement of traffic rules at those places, which would reduce speed and stimulate awareness by the drivers. Decreasing wildlife killing could positively impact human population welfare ([illegible]) and increase the value of ecosystem services provided by green areas to the human population ([illegible]). The welfare increase of the human population is especially true for capybaras since collisions with this animal have caused human causalities ([illegible]), being the primary wildlife species involved in vehicle collisions in Brazil ([illegible]).

Many studies have demonstrated changes in animal behavior in response to road presence, including avoidance and consequently disruption in gene flow within the population ([illegible]). This avoidance generally increases with traffic flow, and can vary with the time of day, week and between months ([illegible]). A complementary approach to this study is to track animals with GPS radio collar, with the purpose of estimating road crossing rate and to have more accurate information on where to install mitigation measures. This telemetry dataset would help discover patterns in animal movement and how they respond to persistent human disturbance ([illegible]).

5. Conclusions

We found that hotspots of road kills occurred near parks, and their presence there can be explained by these environments being preferred by capybaras. Distance to parks and water bodies, traffic flow and green areas, in this order, helped predict the occurrence of capybara road kills and the best location for mitigation measures. For reducing wildlife vehicle collisions in reticulated system like cities, could be done aiming methods to reduce traffic speed, especially that's modifying the user behavior, like warning signal with combination of speed bump.

CRediT authorship contribution statement

Ana Carolina França Balbino Da Silva: Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Jorge Fernando Saraiva De Menezes:** Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Luiz Gustavo Rodrigues Oliveira Santos:** Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Almeida, A. M. R., Arzua, M., Trindade, P. Q. S., A. S. capivaras (*Hydrochoerus hydrochaeris*, Linnaeus, 1766) (Mammalia: Rodentia) em áreas verdes do município de Curitiba (PR). *Estudos em Biologia, 35*(84), 9–16. http://doi.org/ 10.7213/estud.biol.7845.

Almeida, A. R., & Biondi, D. (2014). Área de uso de *hydrochoerus hydrochaeris* L. em ambiente urbano. *Ciencia Animal Brasileira, 15*(3), 369–376.

Angerami, R. N., Câmara, M., Pacola, M. R., Rezende, R. C. M., Duarte, R. M. R., Nascimento, E. M. M., & Silva, L. J. (2012). Ticks and Tick-borne Diseases Features of Brazilian spotted fever in two different endemic areas in Brazil. *Ticks and Tick-Borne Diseases, 3*(5-6), 345–347.

Balkenhol, N., & Waits, L. P. (2009). Molecular road ecology: Exploring the potential of genetics for investigating transportation impacts on wildlife. *Molecular Ecology, 18*, 4151–4164.

Bauni, V., Anfuso, J., & Schivo, F. (2017). Mortalidad de fauna silvestre por atropellamientos en el bosque atlántico del Alto Paraná. *Ecosistemas, 26*(3), 54–66. http://doi.org/ 10.7818/ECOS.2017.26-3.08.

Beckmann, J. P., Clevenger, A. P., Huijer, M. P., & J.A, H. (2010). Safe passages: Highways, wildlife, and habitat connecticity. *Journal of Mammology, 92*(5), 1140–1141. https://doi.org/10.7868/s0030015741010117.

Bratman, G. N., Hamilton, J. P., Hahn, K. S., Daily, G. C., & Gross, J. J. (2015). Nature experience reduces rumination and subgenual prefrontal cortex activation. *Proceedings of the National Academy of Sciences, 112*(28), 8567–8572.

Bruinderink, G. W. T. A. G., & Hazebroek, E. (1996). Ungulate Traffic Collisions in Europe. *Conservation Biology, 10*(4), 1059–1067.

Bueno, C., Sousa, O. M., & Freitas, S. R. (2015). Habitat or matrix : Which is more relevant to predict road-kill of vertebrates ? *Brazilian Journal of Biology, 75*(4), 228–238.

Bueno, C., Faustino, M. T., & Freitas, R. S. (2013). Influence of landscape characteristics on capybara road-kill on highway BR-040, Southeastern Brazil. *Oecologia Australis, 17*(2), 130–137.

Caceres, N. C. (2011). Biological characteristics influence mammal road kill in an Atlantic Forest – Cerrado interface in south-western Brazil Forest – Cerrado interface in south-western Brazil. *Italian Journal of Zoology, 78*(3), 379–389.

Cáceres, N. C., Hannibal, W., Freitas, D. R., Silva, E. L., Roman, C., & Casella, J. (2010). Mammal occurrence and roadkill in two adjacent ecoregions (Atlantic Forest and Cerrado) in south-western Brazil. *Zoologia, 27*(5), 709–717.

Case, R. M. (1978). Interstate highway road-killed animals: A data source for biologists. *Wildlife Society Bulletin, 6*(1), 8–13.

Crawford, B. A., Maerz, J. C., Nibbelink, N. P., Buhlmann, K. A., Norton, T. M., & Albeke, S. E. (2014). Hot spots and hot moments of diamondback terrapin road-crossing activity. *Journal of Applied Ecology, 51*, 367–375.

Díaz, S., Fargione, J., Iii, F. S. C., & Tilman, D. (2006). Biodiversity Loss Threatens Human Well-Being. *PloS Biology, 4*(8).

Dodd, N. L., Gagnon, J. W., Boe, S., & Schweinsburg, R. E. (2007). Assessment of Elk Highway Permeability by Using Global Positioning System Telemetry. *Journal of Wildlife Management, 71*(4), 1107–1117.

Dornas, R. A. P., Kindel, A., Bager, A., & Freitas, S. R. (2012). Avaliação da mortalidade de vertebrados em rodovias no Brasil. In *Ecologia de Estradas: Tendências e Pesquisas* (pp. 139–152).

Epps, C. W., Palsbøll, P. J., Wehausen, J. D., Roderick, G. K., II, R. R. R., McCullough, D. R., & McCullough1 (2005). Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters, 8*, 1029–1038. https://doi.org/10.1111/j.1461-0248.2005.00804.x.

Ferraz, K. M. P. M. D. B., Lechevalier, M.-A., Couto, H. T. Z. Do, & Verdade, L. M. (2003). Damage caused by capybaras in a corn Field. *Scientia Agricola, 60*(1), 191–194. https://doi.org/10.1590/S0103-90162003000100029.

Forman, R. T. T. (2008). *Urban regions: Ecology and planning beyond the city*. Harvard University (1th ed.). Cambridge University Press.

Forman, R. T. T., & Alexander, L. E. (1998). Roads and Their Major Ecological Effects. *Annual Review of Ecology and Systematics, 29*(1), 207–231.

Gagnon, J. W., Theimer, T. C., Dodd, N. L., Boe, S., & Schweinsburg, R. E. (2007). Traffic Volume Alters Elk Distribution and Highway Crossings in Arizona. *Journal of Wildlife Management, 71*(7), 2318.

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2009). A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning, 91*(1), 1–7.

Gunson, K. E., & Teixeira, F. Z. (2015). Road–wildlife mitigation planning can be improved by identifying the patterns and pro- cesses associated with wildlife-vehicle collisions. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of road ecology* (pp. 101–109).

Hartmann, P. A., Hartmann, M. T., & Martins, M. (2011). Snake Road Mortality in a Protected Area in the Atlantic Forest of Southeastern Brazil. *South American Journal of Herpetology, 6*(1), 35–42.

Herrera, E. A., Salas, V., Congdon, E. R., Corriale, M. J., & Tang-Martínez, Z. (2011). Capybara social structure and dispersal patterns: Variations on a theme. *Journal of Mammalogy, 92*(1), 12–20.

Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment, 83*, 195–213.

Hurlbert, A. H., & Haskell, J. P. (2003). The effect of energy and seasonality on avian species richness and community composition. *American Naturalist, 161*(1), 83–97.

Jacobson, S. L., Bliss-ketchum, L. L., De Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere, 7*, 1 15

Khattak, A. J. (2003). Human Fatalities in Animal-Related Highway Crashes. *Transportation Research Record, 1840*(1), 158–166.

Kim, C., Park, Y., & Sang, S. (2008). Spatial and Temporal Analysis of Urban Traffic Volume. In *Poster session presentation in the ESRI International User Conference*, San Diego, CA.

Lesbarrères, A. D., Primmer, C. R., Lodé, T., & Merilä, J. (2006). The effects of 20 years of highway presence on the genetic structure of *Rana dalmatina* populations. *Écoscience, 13*(4), 531–538.

Lesbarrères, D., & Fahrig, L. (2012). Measures to reduce population fragmentation by roads: What has worked and how do we know? *Trends in Ecology and Evolution, 27* (7), 374–380.

Litvaitis, J. A., & Tash, J. P. (2008). An approach toward understanding wildlife-vehicle collisions. *Environmental Management, 42*(4), 688–697.

Lowry, H., Lill, A., & Wong, B. B. M. (2013). *Behavioural responses of wildlife to urban, 88*, 537–549.

Maschio, A. G. F., Santos-costa, M. C., & Prudente, A. L. C. (2016). Road-Kills of Snakes in a Tropical Rainforest in the Central Amazon Basin, Brazil, *11*(1), 46–53. https://doi.org/10.2994/SAJH.

Medeiros, S. S., & Oliveira-Santos, L. G. R. (2018). *Programa de Pós Graduação em Ecologia e Conservação Área de vida, seleção de habitat e atividade diária de capivaras vivendo em uma área urbana*. Campo Grande, Mato Grosso do Sul: Universidade Federal de Mato Grosso do Sul. Retrieved from http://posgraduacao.ufms.br/portal/trabalhos?b_curso_nome=&b_nivel_id=&b_trab_titulo=Área+de+vida%2C+seleção+de+habitat+e+atividade+diária+de+capivaras+vivendo+em+uma+área+urbana&b_trab_area=&b_trab_orientador=&b_trab_aluno=&b_trab_data_de=&b_trab_data_at.

Moreira, J. R., Ferraz, K. M. P. M. B., Herrera, E. A., & Macdonald, D. W. (2013). *Capybara: Biology, use and conservation of an exceptional neotropical species.*
Norton, B. A., Evans, K. L., & Warren, P. H. (2016). Urban Biodiversity and Landscape Ecology: Patterns, Processes and Planning. *Current Landscape Ecology Reports, 1*(4), 178–192.
Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J., Tucker, C. J., Stenseth, N. C., & Lyon, C. B. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution, 20*(9), 503–510.
Planillo, A., & Malo, J. E. (2018). Infrastructure features outperform environmental variables explaining rabbit abundance around motorways. *Ecology and Evolution, 8*, 942–952.
Ramp, D., & Roger, E. (2008). Frequency of animal-vehicle collisions in NSW. In D. Lunney, A. Munn, & W. Meikle. (Eds.), *Too Close for Comfort: Contentious Issues in Human–Wildlife Encountes* (pp. 118–126).
R Core Team. (2020). R: A language and environment for statistical computing. *R Foundation for Statistical Computing.*
Lovelace, R., & Ellison, R. (2018). stplanr: A Package for Transport Planning. *The R Journal, 10*(2).
Root-bernstein, M., & Svenning, J. (2017). Restoring connectivity between fragmented woodlands in Chile with a reintroduced mobile link species. *Perspectives in Ecology and Conservation, 15*(4), 292–299.
Rowland, M. M., Wisdom, M. J., Johnson, B. K., & Kie, J. G. (2000). Elk distribution and modeling in relation to roads. *Journal of Wildlife Management, 64*(3), 672–684. https://doi.org/ 10.2307/3802737.
Rytwinski, T., Soanes, K., Jaeger, J. A. G., Fahrig, L., Findlay, S., Houlahan, J., & Van Der Grift, E. A. (2016). How Effective Is Road Mitigation at Reducing Road-Kill ? A Meta-Analysis. *PLoS ONE, 11*, 1–25.
Schwartz, A. L. W., Williams, H. F., Chadwick, E., Thomas, R. J., & Perkins, S. E. (2018). Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology, 4* (1), 1–7.
Thomas M. Pojar, Richard A. Prosence, D. F. R. and T. N. W. (1975). Effectiveness of a Lighted, Animated Deer Crossing Sig. *Wiley on Behalf of the Wildlife Society, 39*(1), 87–91. http://doi.org/ 10.2307/3800469.
Tigas, L. A., Van Vuren, D. H., & Sauvajot, R. M. (2002). Nd-Fe-B-Magnete.pdf. *Biological Conservation, 108*, 299–306.
Trombulak, S. C., & Frissell, C.a. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology, 14*(1), 18–30.
Xie, Z., & Yan, J. (2008). Kernel density estimation of traffic accidents in a network space. *Computers, Environment and Urban Systems, 32*(5), 396–406.
Yu, W., Ai, T., Shao, S. (2015). District using network kernel density estimation. *Journal of Transport Geography, 45*, 32–47. https://doi.org/10.1016/j.jtrangeo.2015.04.008.

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Space use and activity of capybaras in an urban area

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Due to the rapid growth of urban environments, interactions between animals and humans in cities are increasingly common. Large mammals, such as capybaras (*Hydrochoerus hydrochaeris*), provide benefits to people and biodiversity of urban areas, but can also result in conflicts, such as animal–vehicle collisions or disease transmission. As a consequence, understanding the space use of urban capybara, and the effect of human activity on capybaras, is conducive to the promotion of coexistence. We studied the home range and the role of human disturbance on activity and habitat selection of urban capybaras in the city of Campo Grande (Brazil). We monitored nine groups of capybaras living at four parks: two parks subjected to high human visitation on workdays and two on weekends. Home range of the urban capybaras in the study is larger than those reported in previous studies of wild capybaras. The capybaras under study presented a bimodal activity pattern, which was delayed on days of high human presence, increasing animals' nocturnality. In addition, habitat selection was completely altered on days of high human presence, leading animals to increase avoidance of urban areas and reversing the selectivity patterns for forests, grasslands, and water bodies, that capybaras show on days with low human presence. Even when completely surrounded by an anthropic environment, our results indicate that a mosaic of grasslands near a water body and forested areas will allow capybaras to maintain daily activity and large home ranges. However, human presence significantly altered the daily activity patterns and habitat selection of capybara. Urban planners should account for these data to improve the coexistence of capybaras with humans and thereby minimize the potential for conflicts.

Key words: habitat mosaic, habitat selection, home range, *Hydrochoerus hydrochaeris*, movement, Rodentia, social mammals, urban areas

Devido ao rápido crescimento dos ambientes urbanos, a interação entre animais e humanos nas cidades é cada vez mais comum. Os grandes mamíferos, como as capivaras (*Hydrochoerus hydrochaeris*), proporcionam benefícios às pessoas e à biodiversidade das áreas urbanas, mas também podem acarretar conflitos, como colisões com veículos ou transmissão de doenças. Portanto, compreender o uso do espaço pela capivara urbana e o efeito da atividade humana são necessários para promover a coexistência. Estudamos a área de vida e o papel da perturbação humana na atividade e seleção de habitats de capivaras urbanas na cidade de Campo Grande (Brasil). Monitoramos nove grupos de capivaras que vivem em quatro parques, dois parques sujeitos à alta visitação humana nos dias úteis e dois nos finais de semana. A área de vida das capivaras urbanas estudadas é maior do que as relatadas em estudos anteriores para capivaras selvagens. As capivaras estudadas apresentaram um padrão de atividade bimodal, que foi atrasado em dias de alta presença humana, aumentando a noturnalidade dos animais. Além disso, a seleção de habitat foi completamente alterada em dias de alta presença humana, levando os animais a evitar áreas pavimentadas e revogando os padrões de seleção de florestas, pastagens e corpos d'água que as capivaras mostram em dias com baixa presença humana. Mesmo inseridos em um ambiente completamente antrópico, nossos resultados indicam que um mosaico de pastagens próximo a áreas de corpos d'água e florestas permite que as capivaras desenvolvam sua atividade diária, atingindo grandes áreas de vida. No entanto, a presença humana altera significativamente os padrões de atividade e seleção de habitat. Os planejadores urbanos deveriam considerar estas informações para melhorar a coexistência de capivaras com os seres humanos e minimizar seus conflitos.

Palavras-chave: área de vida, áreas urbanas, *Hydrochoerus hydrochaeris*, mamíferos sociais, mosaico de habitat, movimento, Rodentia seleção de habitat

Over recent decades, the human population has grown at unprecedented rates and—for the first time on Earth's history—most human inhabitants of the planet live in urban areas (Grimm et al. 2008; Stolnitz 2008). The number of species that occurs within a city reflects a balance between local diversity and the city's structural and environmental traits (e.g., green areas, water resources, afforestation, densification, buildings, and streets—Aronson et al. 2014). Within cities, green areas, parks, and urban gardens enhance the richness and diversity of plants, invertebrates, and vertebrates (Fuller et al. 2007). Although most species cannot persist in urban areas (Evans et al. 2011), there are those that can, and those that even may benefit from urbanization (Kark et al. 2007). To assess the role of city conservation, one must understand the ecology of urban fauna and inform urban planners and policymakers accordingly (Norton et al. 2015; Dear and Scott 2018).

The capybara (*Hydrochoerus hydrochaeris*) is an example of an urban adapted species. These herbivorous and semiaquatic mammals occur in South America, from Panama to Argentina (Doumecq Milieu et al. 2012). They are gregarious and organized in hierarchical groups (Moreira and MacDonald 1997; Moreira et al. 2012). Capybaras use water bodies to mate, thermoregulate, and avoid predators, and often live near ponds, lakes, rivers, and swamps (Ojasti 1973; Mones and Ojasti 1986). Moreover, their habitats are commonly surrounded by some forested or bush area—locations in which to rest and hide—and some grasslands in which to feed (Alho and Rondon 1987). In some locations at the present time, they also inhabit large urban centers: in some Brazilian cities, it is common to observe them grazing in green urban areas (Paglia et al. 2012).

Despite being uncommon, some large social herbivores—such as deer and capybaras—live in cities (Díaz et al. 2011). While animals fill unique ecosystem roles (Andersson et al. 2015), there are trade-offs in living with urban capybaras (Marchini and Crawshaw 2015). On the one hand, exposure to nature increases the psychological wellness of humans (Bratman et al. 2015), and contact with animals is particularly valuable (Curtin 2009). As a result, a walk through a park with capybaras potentially can benefit the mood and mental health of people. In addition, having animals such as capybaras present increases the value of recreational ecosystem services provided by green areas to the urban population (Díaz et al. 2011). On the other hand, capybaras also can damage agricultural fields or gardens (Moreira et al. 2001; Ferraz et al. 2003), cause animal–vehicle collisions (e.g., Huijser et al. 2013), and are the principal host of Brazilian spotted fever, a zoonotic tick-borne disease that results in more than 50 deaths in Brazil annually (Angerami et al. 2012; Sakai et al. 2014; de Oliveira et al. 2016). Management actions based on the ecology of capybaras are required to solve these conflicts. However, we cannot rely on knowledge of their basic ecology in natural areas because of the likelihood that it probably will be different in urban areas. Animals living in urban environments tend to extend their activity periods (Dominoni et al. 2014; Da Silva et al. 2015), reduce foraging time (Presley et al. 2009), reduce terrestrial displacement based to human footprint (Tucker et al. 2018), and—as happens in many mammals species—increase nocturnality (Gaynor et al. 2018). It therefore is necessary to study the ecology of urban capybaras to know how they use available habitats as well as their hours of activity so as to inform policymakers and enhance human coexistence with animals in cities.

To better understand the ecology of capybara interacting with humans and fill the knowledge gap regarding ecology of urban capybara, we carried out a study on activity patterns and habitat selection of capybaras living in an urban landscape. We assessed the use of space and activity patterns of urban capybaras and the impact of human disturbance on these processes. Our goals were to: (i) estimate home range sizes of social groups of capybaras and compare them with previously published studies of capybaras living in natural environments; (ii) describe urban capybara activity patterns and address the influence of human disturbance on them; and (iii) describe the daily variation in habitat selection of capybaras and how human presence may modify it. To carry out the foregoing, we monitored nine groups of capybaras living in Campo Grande, the capital of Mato Grosso do Sul state (Brazil). We formulated three hypotheses. Because green areas within cities are fragmented, we hypothesized that capybaras' home ranges would be smaller in urban than natural areas. Secondly, due to human disturbance during daytime, we hypothesized that they would be more active at night and that days with high human presence would alter their daily activity patterns, probably extending the activity to be more nocturnal than on days with low human disturbance. Finally, we hypothesized that capybaras would select different habitat types throughout the day to cover different needs, avoiding urban areas, particularly on days with higher human presence. Our results were designed to lead to conclusions about home range, habitat selection, and activity of urban capybaras that can be used to design parks and other urban green areas. Whether policymakers want to maintain and improve capybaras' populations—to enhance their social and ecological benefits—or whether they want to control capybaras and minimize problems associated with them, we provide data that can contribute to manage these animals within cities.

Materials and Methods

Study area.—We carried out the study in the city of Campo Grande, capital of the state of Mato Grosso do Sul, Brazil (20.469°S, 54.620°W). Campo Grande occupies an area of 8,096 km² and has an estimated human population of 875,000. The city has several green areas within its urban perimeter, which allows for the existence of a diverse vertebrate fauna. We studied capybaras in four green spaces with water bodies and surrounding vegetation (Fig. 1): (1) Nações Indígenas State Park (20.452°S, 54.572°W; Site 1); (2) Sóter Ecological Municipal Park (20.429°S, 54.575°W; Site 2); (3) Coronel Ernesto Geisel Avenue (20.503°S, 54.640°W, Site 3), and (4) the Private Reserve of the Federal University of Mato Grosso do Sul (20.503°S, 54.613°W; Site 4). Capybaras live within the parks and seldom venture beyond their borders.

Site 1 is the largest urban park of the city (119 ha), formed of large grassland areas and a large riparian forest (~6 ha; white patch in Fig. 1), crossed by a stream that connects a water reservoir (0.39 ha) with an artificial lake (4.68 ha; black patch on the left of Site 1; see Fig. 1). Site 2 (22 ha) also presents large grassland areas and a riparian forest area (3 ha) crossed by a stream that runs through the park to a city avenue (Fig. 1). Site 3 is the most urbanized of the study area: a long (~12 km) and busy avenue crossed by a stream (black line of Site 3; see Fig. 1). The group of capybaras monitored at Site 3 live in a part of the avenue where the stream's shores contain a grassland band (~5 m wide) and a thin riparian forest (Fig. 1). Site 4 (~57 ha) is located at the campus of the Federal University of Mato Grosso do Sul. It is crossed by streams (black lines in Fig. 1) ending in an artificial lake (~7.65 ha; black patch of Fig. 1) surrounded by riparian and savanna forest areas (65.3 ha; white patches of Fig. 1) and grasslands (1 ha; gray patches of Fig. 1). Between the university buildings are some large lawn areas (likewise depicted in gray in Fig. 1) where capybaras also graze.

Sites 1 and 2 are recreational parks, where people go to walk, run, ride bicycles, and spend time with their families, being particularly crowded during the weekends. Site 3 is crowded on workdays, when people go to work and study in this part of the city; it is practically empty on weekends. Site 4, the university campus, is similar in that there is a strong human presence (> 20,000 students and employees) on workdays and a practical absence of people during weekends (closed gates with entrance controlled to a limited number of authorized people).

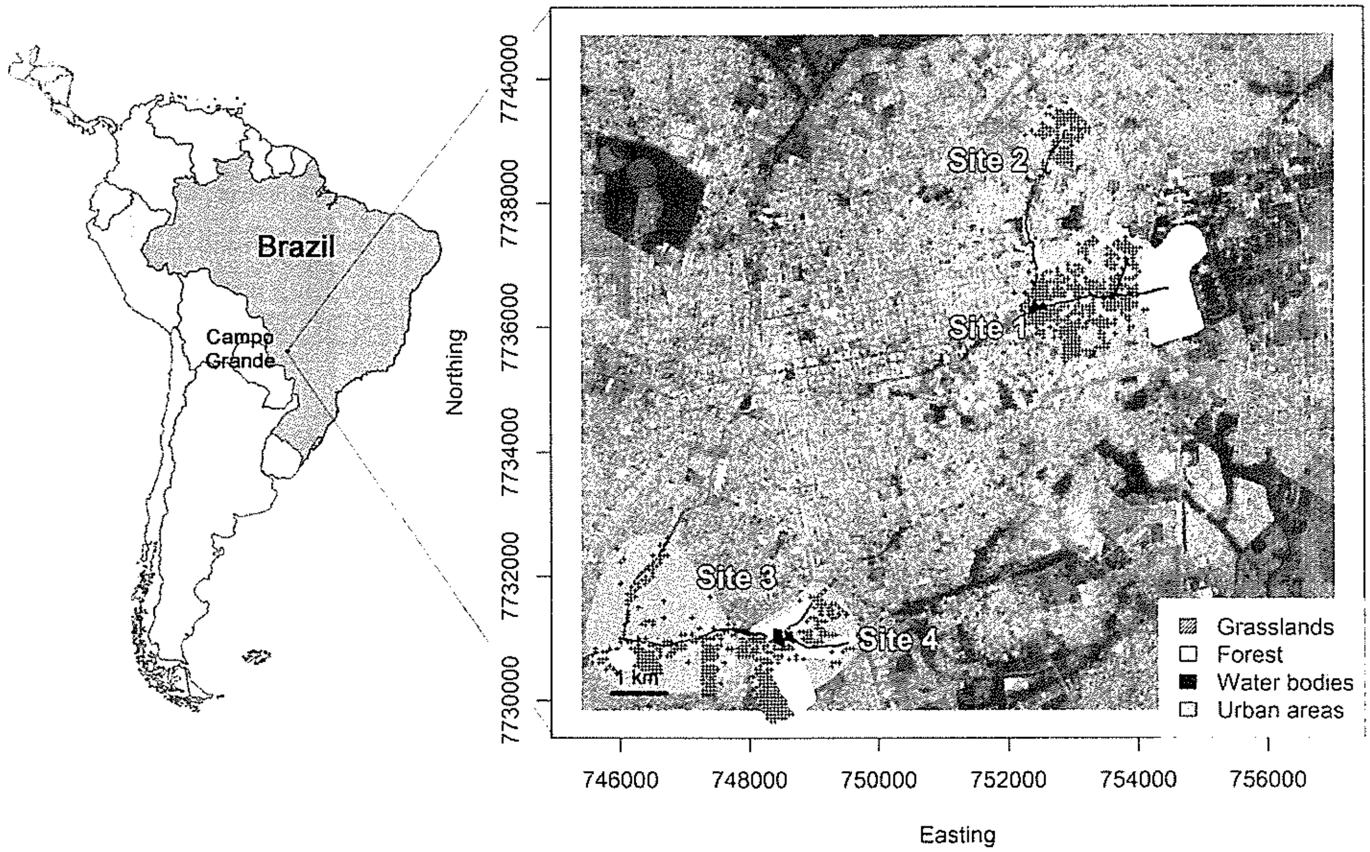

Fig. 1.—Satellite image showing part of the city of Campo Grande (Mato Grosso do Sul, Brazil) where we studied the movement ecology of capybaras (*Hydrochoerus hydrochaeris*). For each site, we depicted the locations where the animals were captured and monitored (small crosses) and the habitat classes.

Capybara capture and tracking.—We captured 15 adult capybaras belonging to nine social groups between December 2016 and November 2017. We used chemical containment by means of an anesthetic solution of Tiletamine (dose: 2 mg/kg) and Zolazepam (dose: 2 mg/kg; Zoletil; Virbac, Hamilton, New Zealand). The solution was intramuscularly administered by launching a dart from a CO_2 injection rifle (model JM.DB.13; DAN-INJECT ApS, Kolding, Denmark). The anesthetic solution takes between 5 and 15 min to take effect, during which time the capybaras could fall into the water or be hit by a vehicle. To avoid those eventualities, we shot the individuals far from water bodies and urban roads. When the animals were completely anaesthetized, we identified the sex, weighed, marked them with numbered colored earrings, and equipped them with tracking GPS collars (Tigrinus Equipamentos para Pesquisa Ltda., Timbó, Santa Catarina, Brazil). During this process, a veterinarian checked the vital parameters of the individuals (heart rate, respiratory rate, rectal temperature, muscle tone, and auricular, ocular, and anal sphincter reflex) every 10 min. At these 10-min intervals, the veterinarian also checked for ectoparasites, wounds, and other signs that could compromise animal health. Procedures followed ASM guidelines (Sikes et al. 2016) and were authorized by the Ethics Committee on the Use of Animals, number 676/2015, and by the Authorization System and Information on Biodiversity number 49802. Each GPS collar was programmed to record geographical location, date, and time, every 30 min. We programmed the collars to send the data once a month, so we remotely downloaded the data monthly using an antenna and UHF receiver (Tigrinus Equipamentos para Pesquisa Ltda.).

Cover types of the studied areas.—For the four studied areas, we classified the habitats using the Google Earth Pro software. We manually delimited classes of land-use polygons (habitat classes) of four biologically relevant categories for capybaras: (1) grassland areas; (2) forest vegetation areas; (3) water bodies; and (4) urban areas (i.e., paved areas, including buildings, avenues, streets, and sidewalks; Fig. 1). Three of these habitat types are ecologically relevant for the different daily activities of capybaras: grasslands to feed, forests for rest and shelter, and water bodies to thermoregulate, avoid predation, and mate (Ojasti 1973; Mones and Ojasti 1986). The other, urban areas, is included because it is present for human use, and instead is expected to be perceived as a risk area for capybaras' activity rather than as an ecological resource. These categories are distinguishable easily by the naked eye using high-resolution satellite images. However, in instances of doubt, we used the Google Street View to confirm the habitat classification.

Home range estimation.—We used three estimators of home ranges: (1) Minimum Convex Polygon (MCP 95%—Mohr 1947), calculated from 95% of the GPS locations; (2) Kernel Density Probability (KDE—Worton 1989); and (3) Kernel Brownian Bridge (BBMM—Bullard 1999). We estimated the KDE and BBMM using the 95% isopleth of probability, reference smoothing parameter (*href*), GPS error of 20 m (*sig 1*), and diffusion parameter (*sig 2*) calculated by maximum likelihood. The MCP, because it only estimates the contour, assumes the animal uses the area uniformly, is highly sensitive to outliers and may incorporate nonused areas into the home range estimation. The KDE calculates the probability of utilization of each point, but ignores the temporal sequence of consecutive locations. The BBMM incorporates the temporal structure of consecutive locations to the kernel estimation, providing better outcomes of the paths used by animals within their home ranges. We calculated the three estimators to obtain a better understanding of how urban capybara use their home ranges (BBMM and KDE) and compare the home range sizes with previously published studies (MCP and KDE). Because home range size is positively related to monitoring time, we plotted monitoring time against home range size to ensure the individuals had reached an asymptote on home range size to be included in the study.

Because capybaras move in groups, we first assessed the degree of cohesion of group movement to estimate the number of individuals that would lead to reliable representations of home range size of the groups. To test this, we simultaneously [illegible]tured eight individuals of two social groups (four from each group) living at Site 4 (Fig. 1). We used the overlap between home ranges (considering all monitoring days, reported in Table 1) of the individuals (estimated by the MCP) as a proxy for the degree of cohesion of the group. We assumed an overlap of ≥ 80% as a reasonably indication of a high degree of cohesion to use of one individual per group of capybaras as a proxy of group home range estimations.

All analyses in this study were undertaken in the R environment (R Development Core Team 2018). We carried out the home range analyses using the *adehabitatHR* package (Calenge 2011). Group cohesion was high (see "Results"), so we ruled that one capybara from each group was representative of the entire area used by its group. Thus, apart from the eight individuals from Site 4 (groups G1 and G4), we monitored an additional seven individuals representing seven groups: five individuals at Site 1 (G3, G6, G7, G8, G9), one from Site 2 (G5), and one from Site 3 (G2) (see Table 1). From G1 and G4, we chose the animal that was monitored the longest (G1[illegible]3 and G4-ID2) as representatives of the group to calculate mean home range size. To compare the home range sizes of animals from urban environments with those of animals from natural environments, we searched the Web of Science platform for articles related to the capybara home ranges using the following key words: home range, home range size, capybaras, and rodents, both in English and in Portuguese. We found four articles fitting the search parameters and made a table containing the values of home range sizes of the animals from the literature and the values of our studied urban capybaras.

Daily activity.—We used the Euclidean distance between locations of capybaras at hourly periods as a proxy of activity. Human disturbance was coded daily as a binary covariate according to human visitation of studied parks (0 = closed/low visitation, 1 = open/intense visitation). For instance, at recreational parks, weekends (Saturday and Sunday) were considered as intense visitation (coded as 1), and workdays (Monday through Friday) as low visitation (coded as 0). Time of day

Table 1.—Average individuals home range sizes of capybaras (*Hydrochoerus hydrochaeris*) studied here and that from data published in the literature. The first column, *N*, represents the mean number of individuals of the group. ID is the identification number, being G the group. BBMM = Kernel Brownian Bridge; MCP = Minimum Convex Polygon.

N	Home range size (ha)			Country	Environment	Reference	ID	Method	Temp. resol.	Monitoring time (days)
	MCP	Kernel	BBMM							
10.9	8.15			Venezuela	Farm	MacDonald (1981)		Direct obs.	1 loc./h	~365
18.1	10.4			Venezuela	Farm	Herrera and MacDonald (1989)		Direct obs.	1 loc./h	~365
31.5	16.93			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
33.6	27.46			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
27.8	14.63			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
35.6	22.57			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
33.3	27.6			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
31.6	11.3			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
29.3	23.71			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
25.8	15.78			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
31.5	12.34			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
25.8	17.27			Argentina	Natural park	Corriale et al. (2013)		Direct obs.	2 loc./h	730
	437	193		Paraguay	Biological reserve	Campos-Krauer et al. (2014)		VHF	~2 loc./day	~35
	492	421		Paraguay	Biological reserve	Campos-Krauer et al. (2014)		VHF	~2 loc./day	83
	737	52		Paraguay	Biological reserve	Campos-Krauer et al. (2014)		VHF	~2 loc./day	187
	484	62		Paraguay	Biological reserve	Campos-Krauer et al. (2014)		VHF	~2 loc./day	387
	997	198		Paraguay	Biological reserve	Campos-Krauer et al. (2014)		VHF	~2 loc./day	469
	352	176		Paraguay	Biological reserve	Campos-Krauer et al. (2014)		VHF	~2 loc./day	
12.5	62.13	54.69	38.91	Brazil	Urban park (Site 4)	This study	G1-ID1	GPS	2 loc./h	24
12.5	19.48	19.8	29.48	Brazil	Urban park (Site 4)	This study	G1-ID2	GPS	2 loc./h	54
12.5	60.02	47.09	43.37	Brazil	Urban park (Site 4)	This study	G1-ID3	GPS	2 loc./h	97
12.5	32.09	43.85	32.3	Brazil	Urban park (Site 4)	This study	G1-ID4	GPS	2 loc./h	12
	104.93	71.51	47.68	Brazil	Urban park (Site 3)	This study	G2	GPS	2 loc./h	122
46.3	30.76	33.7	29.11	Brazil	Urban park (Site 1)	This study	G3	GPS	2 loc./h	54
49	23.87	27.73	30.18	Brazil	Urban park (Site 4)	This study	G4-ID1	GPS	2 loc./h	53
49	18.06	16.16	19.67	Brazil	Urban park (Site 4)	This study	G4-ID2	GPS	2 loc./h	131
49	8.68	17.2	14.95	Brazil	Urban park (Site 4)	This study	G4-ID3	GPS	2 loc./h	4
49	20.94	18.8	27.68	Brazil	Urban park (Site 4)	This study	G4-ID4	GPS	2 loc./h	47
25	31.96	30.16	30.21	Brazil	Urban park (Site 2)	This study	G5	GPS	2 loc./h	15
45.1	59.67	48.43	47.31	Brazil	Urban park (Site 1)	This study	G6	GPS	2 loc./h	145
50.2	35.99	33.92	33	Brazil	Urban park (Site 1)	This study	G7	GPS	2 loc./h	114
37.2	13.48	10.9	14.9	Brazil	Urban park (Site 1)	This study	G8	GPS	2 loc./h	157
27.4	7.16	10.29	14.58	Brazil	Urban park (Site 1)	This study	G9	GPS	2 loc./h	53

is modeled as sine and cosine harmonics [cos(hours * 2 * pi/24) and sin(hours * 2 * pi/24)] to allow for expected nonlinear (e.g., bimodal) effects. We tested the effect of time of day and human disturbance on capybara daily activity using a Linear Mixed Model with temporal autocorrelation, available in the *lme4* package (Kuznetsova et al. 2017). Because of the nested structure of our data, we included a random effect where sampled hours were nested within days, and then within individuals. Finally, we controlled by temporal autocorrelation between successive hours within each day of each individual using a first-order autoregressive structure; i.e., activity values of determined hours of one individual were affected by the hour immediately before. We used square roots of distance moved to achieve residuals' normality.

Habitat selection.—As with home range analyses, we used data from nine of the 15 tracked individuals (one individual per group) to carry out a Step Selection Function (SSF) analysis. The criterion of inclusion was to be the individual monitored for the longest time periods for G1 and G4 (G1-ID3 and G1-ID2, respectively) and the individuals representing the remaining groups (see Table 1). We estimated the strength of selection of the four habitat types, as well as their hourly changes throughout the day, using the SSF approach. The SSF is a variation of the Resource Selection Function (RSF—Manly et al. 2007) that explicitly incorporates the process of animal movement. While the RSF estimates the strength of selection as the rate between the use of a certain habitat and its total availability, the SSF estimates this step-by-step. This means that the availability of a certain habitat for one individual depends on its spatial position, given its capacity of locomotion and navigation. We therefore needed to estimate the changes in habitat availability for each step in SSF. For capybaras, we created 30 random (unused) steps starting from each used location, a sampling size able to represent the actual resource availability around animal position in our studied areas. The length and direction of these random steps were calculated from a random distribution of step length (distance between consecutive locations) and turning angles (difference in direction between consecutive steps) for the entire trajectory of each animal. Thus, the arrival habitat of each observed step (used habitat, coded as "1") was compared to 30 potential locations of each random step (available habitats, coded as "0"). For each observed step, we recorded the time of the day and the used and available habitats.

Given the binary nature of the response variable (used = 1, versus available = 0), we solved the SSF using a Conditional Logistic Regression model (CLR—Connolly and Liang 1988) with the *survival* package (Therneau and Lumley 2014). There, habitat type was included as a fixed covariate, and each step of each capybara was included as the stratum or condition (equivalent to a random covariate in a mixed model). This procedure allowed us to compare used and available habitats within each step of each capybara. To test whether the selection strength of each habitat type varied over the course of daily activities, we included an interaction term between the habitat type and the time of the day in the CLR. The time of the day was included in the form of sine and cosine harmonics [cos(hours * 2 * pi/24) and sin(hours * 2 * pi/24)] to allow nonlinear changes in habitat selection strength throughout daily activities (Oliveira-Santos et al. 2016). To test the effect of human disturbance on habitat selection we also included the same binary classification used in the analyses of daily activity pattern (0 = closed/low visitation, 1 = open/intense visitation). Both time of the day and human disturbance were included as interaction terms with habitat type to verify how they trigger changes on habitat selection.

Results

Home range.—The four individuals tracked in each of the two social groups in the Site 4 remained strongly cohesive, presenting home ranges with individual overlap greater than 88% (Fig. 2). This suggests that it is not necessary to monitor more than one individual of the same social group to have an estimate of home range size of the group. The average value of home range sizes were: 40.23 ha (7.16–104.93; MCP), 3[illegible]7 ha (10.29–71.51; Kernel), and 31.09 ha (14.9–47.68; BBMM; Table 1).

Previous studies that estimated the home ranges of nonurban capybaras using the MCP estimator method presented the following mean estimates across individuals: 8.15 ha (MacDonald 1981); 10.4 ha (Herrera and MacDonald 1989); 18.96 ha (Corriale et al. 2013); and 583 ha (Campos-Krauer et al. 2014). The last study also used the Kernel estimator method and presented an average using that estimator of 183.6 ha (Table 1).

Daily activity.—The hourly distance moved by capybaras depended on the hour of the day ($b_{sine1[time\ of\ day]} = -1.00$, $P < 0.01$; $b_{cosine1[time\ of\ day]} = 0.49$, $P < 0.01$; $b_{sine2[time\ of\ day]} = 1.00$, $P < 0.01$; $b_{cosine1[time\ of\ day]} = 0.09$, $P = 0.20$; Figs. 3c and 3d). The daily activity pattern is bimodal, showing two crepuscular peaks of activity, one during dawn and one during dusk, whereas capybaras remain inactive in the morning and afternoon. Human visitation affected the activity in an interaction with the time of the day ($b_{humans\ *\ sine1[time\ of\ day]} = -0.02$, $P = 0.87$; $b_{humans\ *\ cosine1[time\ of\ day]} = 0.25$, $P = 0.01$; $b_{humans\ *\ sine2[time\ of\ day]} = -0.07$, $P = 0.46$; $b_{humans\ *\ cosine2[time\ of\ day]} = -0.47$, $P < 0.01$). Thus, the intense presence of humans in parks did not alter the overall amount of capybara daily activity but delayed its bimodal activity pattern. In comparison with the days of low human visitation, capybaras delayed approximately 1–2 h to begin their dusk activity, compensated with further displacements in the beginning of the night, and kept activity until later in the dawn (Fig. 3d).

Habitat selection.—Capybaras selected different habitats at different times of day, and changed their selection under regimes of higher human disturbance (Figs. 3a and 3b). Forest areas ($b_{forest\ *\ sine[time\ of\ day]} = 1.47$, $P < 0.01$; $b_{forest\ *\ cosine[time\ of\ day]} = 0.93$, $P < 0.01$) and water bodies ($b_{water\ *\ sine[time\ of\ day]} = 1.23$, $P < 0.01$; $b_{water\ *\ cosine[time\ of\ day]} = 0.86$, $P < 0.01$) were selected in early morning to midafternoon, and avoided from midafternoon to midnight (Fig. 3a). Urban areas always were avoided ($b_{urban} = 0.43$, $P < 0.01$), regardless of the time of day, but this avoidance was greater during daytime ($b_{urban\ *\ sine[time\ of\ day]} = 0.85$, $P < 0.01$;

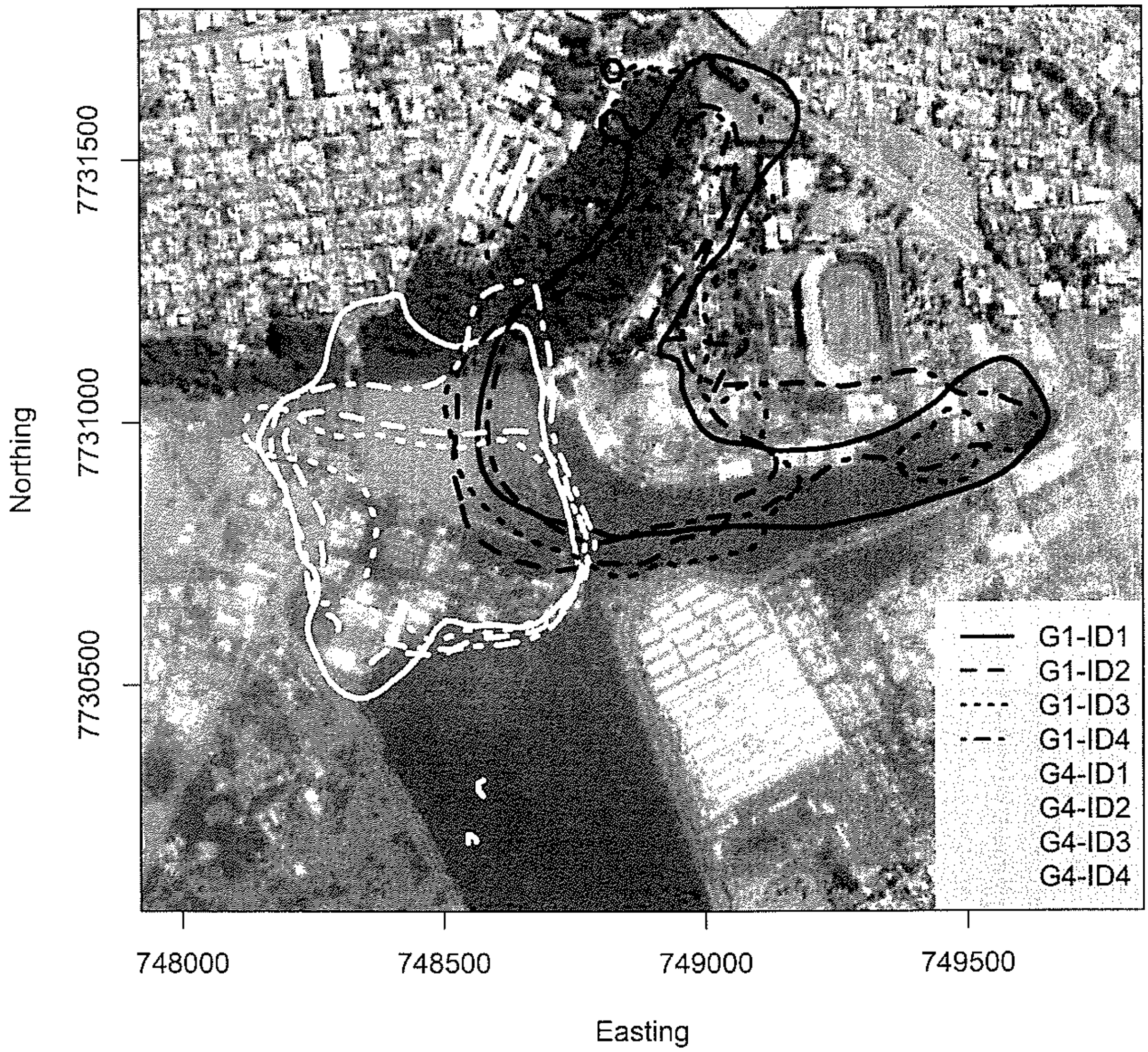

Fig. 2.—Satellite image of Site 4 (Campo Grande, Mato Grosso do Sul, Brazil). Each polygon represents the home range of an individual capybara (*Hydrochoerus hydrochaeris*). The black polygons represent four individuals of the same group (G1). And the white polygons represent four individuals from another group (G4).

$b_{urban * cos(time of day)} = 1.30$, $P < 0.01$; Fig. 3a). Notably, habitat selection of capybaras also was markedly affected by human disturbance. High human visitation triggered avoidance of the usually selected habitats: forest ($b_{forest * humans} = -0.31$, $P < 0.01$) and water bodies ($b_{water * humans} = -0.42$, $P < 0.01$), and drove an even greater avoidance for urban areas ($b_{urban * humans} = -0.25$, $P < 0.01$; Fig. 3b). Note that on days of high disturbance (high human visitation to parks), capybaras just avoided urban areas, while other habitat types selected (forests, water bodies, and grasslands [reference category]) seemed random (Fig. 3b).

Discussion

Urban capybaras exhibited large home ranges, bimodal daily activity patterns, and remarkable changes in habitat selection throughout the day. Moreover, they altered the activity patterns and habitat selection on days with intense human disturbance. The daily activity patterns seemed less affected by human presence than habitat selection, showing a similar (bimodal) pattern both on days with low and high human presence, but with a delay in activity—which resulted in an increase of nocturnality—on days of high human presence. The effect of human disturbance on habitat selection was remarkable, completely altering the daily patterns of selection and avoidance of the different habitat types. On days with low human disturbance, capybaras strongly selected forests and water bodies during the morning and afternoon, and grasslands during the dusk and night. However, on days of intense human presence, capybaras did not select any habitat type and strongly avoided urban areas, particularly during daytime. Our results describe the use of space of urban capybaras living in green areas of a large city, and how human presence triggers changes in their space use.

Contrary to our expectations, our results revealed that home ranges of urban capybaras were larger than those estimated

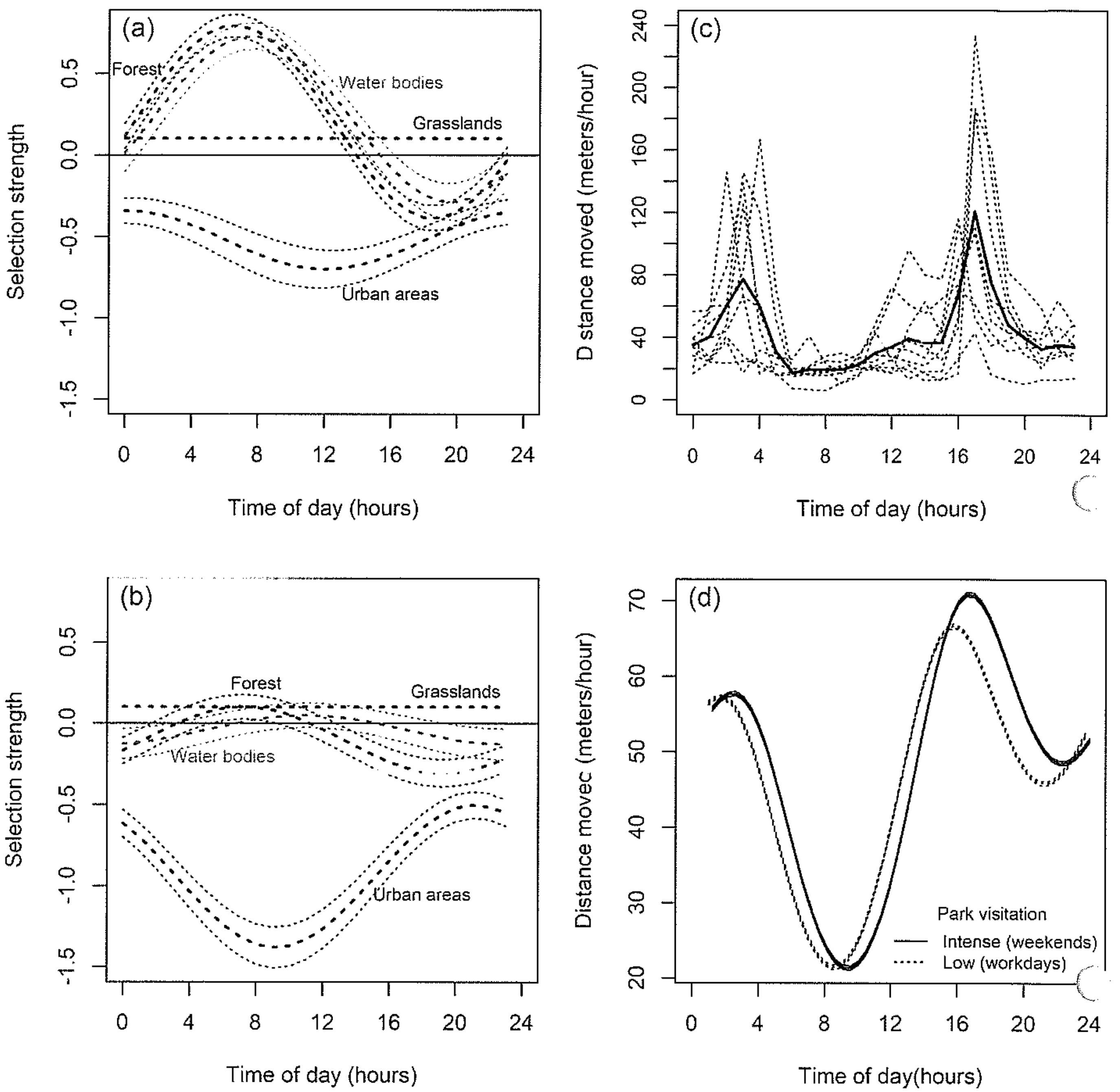

Fig. 3.—Habitat selection and activity patterns of nine groups of capybaras (*Hydrochoerus hydrochaeris*) living in parks of the city of Campo Grande (Mato Grosso do Sul, Brazil). (a) For days with low human visitation, coefficients of habitat selection strength for each studied habitat type along the time of day (hours). Values above the line (positive) represent selection and values below the line (negative) represent avoidance of a certain habitat type (comparing to grasslands, the reference category). The strength section coefficients (dashed line) and their 95% confidence intervals (dotted line) are depicted for each habitat type: forests, water bodies, grasslands, and impervious cover (highly anthropized areas as roads, see the text for more details). (b) Coefficients of habitat selection strength (similar specifications as the previous plot) of the four habitat types during the days of intense human visitation. (c) Real data of the hourly distance moved (as a proxy for activity) of all studied capybaras (including all monitoring days) at different times of the day. Dotted lines are the values of each individual; the bold line is the mean. (d) Estimates of the mixed model of the hourly distance moved (proxy for activity) of studied capybaras during the time of the day at days of intense (bold lines) and low (dashed lines) human visitation of parks.

in natural environments (MacDonald 1981; Herrera and MacDonald 1989; Corriale et al. 2013). This disagrees with the general pattern of mammals reducing the size of their areas of movement when habitats are under effects of large human influence (Tucker et al. 2018). The tendency appears opposite for capybaras. The only exception are capybaras of natural areas of the Chaco (Campos-Krauer et al. 2014), displaying home ranges over five times larger than those from urban areas studied here. The Chaco is a xeric environment with low primary productivity compared to the other studied natural areas (Pozer and Nogueira 2004). Low primary productivity can lead capybaras to travel greater distances to acquire sufficient resources for their energetic demands (Mueller et al. 2011). This also may explain why one studied capybara (ID G2) occupying an area with scarce grasslands showed the largest home range size among monitored individuals. The abundance and easy access of landscape lawns in predator-free anthropic environments, such as the urban locations examined herein, favors the establishment of large groups of capybaras (Ferraz et al. 2007). Living in large groups in areas of high food availability and lacking predators probably would lead capybaras to expand their home ranges (Gering and Blair 1999). In natural environments, capybaras are subjected to higher predation pressures, for example, from jaguars (*Panthera onca*), a major predator of young capybaras (Rengger 1830; Schaller and Vasconcelos 1978). Hence, the absence of predators in large urban centers could allow capybaras to increase their group size and area of movement, consequently increasing their home ranges.

Some species alter their circadian cycle when living in large urban centers due to illumination and/or constant human presence (Luniak 2004; Presley et al. 2009). However, these factors seem not to affect the capybaras in our study. These capybaras exhibited the same activity pattern as those living in natural environments; that is: bimodal activity, being less active in the morning and more active in the afternoon and evening (MacDonald 1981). Even on days of intense human visitation, capybaras maintained this bimodal activity pattern. Despite the bimodal pattern appearing strongly consistent in shape, intense human visitation altered it by delaying the timing of all daily movements. Thus, on days of intense human presence, capybaras started their activity 1–2 h later, turning themselves more nocturnal than on days with low human presence. This delay coincides with the start time and time length of the rush hours of visitation/recreation/human displacement in the four studied areas. Our findings also are in agreement with the consistent trend to nocturnality found for 62 species of mammals in relation to human disturbance (Gaynor et al. 2018). While this shift toward nocturnal activity may facilitate coexistence of capybaras with humans, it can also entail fitness costs to individuals and alter the evolution of urban fauna (Gaynor et al. 2018).

Habitat selection changed markedly in response to human presence. Usually, capybaras select habitats according to: (1) quality of foraging sites; (2) water availability; and (3) presence of shelters and resting places (Corriale and Herrera 2014). In days of low human visitation, urban capybaras selected forest and water habitats and moved less in the dawn and at midday. This change in habitat selection was aligned to the peaks of bimodal activity, suggesting increases in activity are related with changes in habitat selection strategies: (1) when animals leave a forest and/or water body to select grassland habitats in the evening twilight; and (2) when they return from the grassland habitats to select forest vegetation and/or water bodies at dawn. Our findings agreed with the pattern described in natural environments, in which capybaras use forests and water bodies during these periods for resting and thermoregulation (see Lord 1991). Moreover, this result also highlights the importance of the proximity and interaction between these types of selected habitats for the maintenance of capybara populations. The opposite happened with anthropogenic areas, which always were avoided by capybaras. Many animals, such as coyotes, although having larger home ranges in urban than natural environments, also tend to avoid highly anthropogenic places such as commercial areas and roads during certain times of day (Grinder and Krausman 2001; Gese et al. 2012). Avoidance of highly anthropized areas seems a common pattern, even for species that can establish themselves and maintain persistent and abundant populations within cities (Adkins and Stott 1998).

During days of intense visitation by humans to parks, habitat selection was disturbed: capybaras did not show selection for forests and water bodies throughout the day, acting randomly with respect to these habitat types. They selected grasslands at night, but later and with less strength than on days of low human pressure. The effect of human disturbance in avoidance of urban areas of the parks during the daytime was even stronger, with double the strength of avoidance than during days with low human visitation. During the night, avoidance strength of urban areas was similar for days of low and intense park visitation by humans. Our results showed how human presence disturbed the activity of capybaras, both in space and time, with animals avoiding the places and moments where humans most are present. Similar results were found with brown bears inhabiting human-dominated landscapes of Scandinavia (Martin et al. 2010), avian raptor in Spain (Bautista et al. 2004), and different bird species on ocean-exposed sandy beaches of Australia (Meager et al. 2012), suggesting that animals learn to predict the activity of humans to be able to adapt their behavior to avoid them when disturbance is high.

Despite the decline of wild populations and expansion of urban environments (Marzluff et al. 2001), the capybaras we studied established larger home range and kept their group size as large as those found in natural areas. Capybaras, as with coyotes and foxes (Grinder and Krausman 2001; Contesse et al. 2004), are found easily in some urban centers (Verdade and Ferraz 2006; Almeida et al. 2013; Almeida and Biondi 2014). A requisite for their successful establishment is that urban landscapes be able to provide sufficient resources for survival. The presence of urban parks with grasslands, forest vegetation areas, and water bodies certainly contribute to the success of urban capybaras' populations (Corriale and Herrera 2014). The establishment and maintenance of urban capybaras' populations depends on a mosaic of these habitats within urban green areas. Close to one of the studied areas (Site 1) is another urban park (Dos Poderes Park) that presents a larger and better preserved forest, but lacking grasslands and water bodies; capybaras are absent there. We believe that capybaras cannot settle in this park due to the absence of the mosaic of the three habitat types they require. Furthermore, regulation in the number of visitors, mainly during dawn and dusk, could decrease the pressure on capybara daily routines. These regulations may be important mainly if further evidence demonstrates that human-induced changes in activity and habitat selection may decrease their fitness due to restriction of grazing time and/or of accessing grazing areas.

As urban areas continue to expand and natural environments are increasingly fragmented, maintaining green areas in cities is fundamental for biodiversity conservation (McDonald et al. 2008; Goddard et al. 2013). Our study city, Campo Grande, is located in the Brazilian Cerrado, a biodiversity hotspot with more than 160 species of mammals (Myers et al. 2000). Maintaining urban parks therefore allows preserving capybara populations, which provide ecosystem services and allows people to connect with nature, enhancing their well-being (Fuller et al. 2007). Notable aspects to maintaining capybaras in urban areas are: (1) to have parks that are large enough and include a mosaic of three habitat types: water bodies, grasslands, and forest areas; and (2) carefully designing the urban areas where humans walk inside the parks. Our results show that intense human presence disturbed the habitat selection and activity of capybaras, leading them to strongly avoid urban areas during the day. As human urban populations grow, care must be taken to have enough green areas per inhabitant to preclude surpassing the human presence that capybaras can support in adapting their behavior. Understanding the effects of urbanization on the use of space, activity pattern, and habitat selection of capybaras, as well as the environmental characteristics this species requires to live in anthropogenic environments, will allow for precise management actions.

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Literature Cited

Adkins, C. A., and P. Stott. 1998. Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. Journal of Zoology 244:335–346.

Alho, C. J., and N. L. Rondon. 1987. Habitats, population densities, and social structure of capybaras (*Hydrochaeris hydrochaeris*, Rodentia) in the Pantanal, Brazil. Revista Brasileira de Zoologia 4:139–149.

Almeida, A. M. R., M. Arzua, P. W. S. Trindade, and A. S. Junior. 2013. Capivaras (*Hydrochoerus hydrochaeris*, Linnaeus, 1766) (Mammalia: Rodentia) em áreas verdes do município de Curitiba (PR). Estudos de Biologia 35:9–16.

Almeida, A. R., and D. Biondi. 2014. Area de uso de *Hydrochoerus hydrochaeris* L. em ambiente urbano, Curitiba, Paraná, Brasil. Ciência Animal Brasileira 15:369–376.

Andersson, E., et al. 2015. Scale and context dependence of ecosystem service providing units. Ecosystem Services 12:157–164.

Angerami, R. N., et al. 2012. Features of Brazilian spotted fever in two different endemic areas in Brazil. Ticks and Tick-Borne Diseases 3:346–348.

Aronson, M. F., et al. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society of London, B. Biological Sciences 281:20133330.

Bautista, L. M., et al. 2004. Effect of weekend road traffic on the use of space by raptors. Conservation Biology 18:726–732.

Bratman, G. N., J. P. Hamilton, K. S. Hahn, G. C. Daily, and J. J. Gross. 2015. Nature experience reduces rumination and subgenual prefrontal cortex activation. Proceedings of the National Academy of Sciences of the United States of America 112:8567–8572.

Bullard, F. 1999. Estimating the home range of an animal: a Brownian bridge approach. M.S. thesis, Johns Hopkins University, Baltimore, Maryland.

Calenge, C. 2011. Home range estimation in R: the adehabitatHR package. The Comprehensive R Archive Network. http://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf. Accessed 7 February 2021.

Campos-Krauer, J. M., S. M. Wisely, I. K. Benitez, V. Robles, and R. T. Golightly. 2014. Rango de hogar y uso de hábitat de carpinchos en pastizales recién invadido en el Chaco seco de Paraguay. Therya 5:61–79.

Connolly, M. A., and K. Y. Liang. 1988. Conditional logistic regression models for correlated binary data. Biometrika 75:501–506.

Contesse, P., D. Hegglin, S. Gloor, F. Bontadina, and P. Deplazes. 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mammalian Biology 69:81–95.

Corriale, M. J., and E. A. Herrera. 2014. Patterns of habitat use and selection by the capybara (*Hydrochoerus hydrochaeris*): a landscape-scale analysis. Ecological Research 29:191–201.

Corriale, M. J., E. Muschetto, and E. A. Herrera. 2013. Influence of group sizes and food resources in home-range sizes of capybaras from Argentina. Journal of Mammalogy 94:19–28.

Curtin, S. 2009. Wildlife tourism: the intangible, psychological benefits of human–wildlife encounters. Current Issues in Tourism 12:451–474.

Da Silva, A., M. Valcu, and B. Kempenaers. 2015. Light pollution alters the phenology of dawn and dusk singing in common European songbirds. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 370:20140126.

de Oliveira, S. V., et al. 2016. An update on the epidemiological situation of spotted fever in Brazil. The Journal of Venomous Animals and Toxins Including Tropical Diseases 22:22.

Dear, M., and A. J. Scott. 2018. Towards a framework for analysis. Pp. 3–16 in Urbanization and urban planning in capitalist society (M. Dear and A. J. Scott, eds.). Methuen, London, United Kingdom.

Díaz, S., et al. 2011. Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. Proceedings of the National Academy of Sciences of the United States of America 108:895–902.

Dominoni, D. M., E. O. Carmona-Wagner, M. Hofmann, B. Kranstauber, and J. Partecke. 2014. Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. Journal of Animal Ecology 83:681–692.

Doumecq Milieu, R. E., A. Morici, and N. A. Nigro. 2012. Ampliación de la distribución austral del carpincho (*Hydrochoerus hydrochaeris*) en la provincia de Buenos Aires, Argentina. Nótulas Faunísticas 92:1–10.

Evans, K. L., D. E. Chamberlain, B. J. Hatchwell, R. D. Gregory, and K. J. Gaston. 2011. What makes an urban bird? Global Change Biology 17:32–44.

Ferraz, K. M. P. M. D., S. F. D. Ferraz, J. R. Moreira, H. T. Z. Couto, and L. M. Verdade. 2007. Capybara (*Hydrochoerus hydrochaeris*) distribution in agroecosystems: a cross-scale habitat analysis. Journal of Biogeography 34:223–230.

Ferraz, K. M. P. M. D., M. A. Lechevalier, H. T. Z. D. Couto, and L. M. Verdade. 2003. Damage caused by capybaras in a corn field. Scientia Agricola 60:191–194.

Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren, and K. J. Gaston. 2007. Psychological benefits of greenspace increase with biodiversity. Biology Letters 3:390–394.

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

Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532–541.

Gese, E. M., P. S. Morey, and S. D. Gehrt. 2012. Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. Journal of Ethology 30:413–425.

Goddard, M. A., A. J. Dougill, and T. G. Benton. 2013. Why garden for wildlife? Social and ecological drivers, motivations and barriers for biodiversity management in residential landscapes. Ecological Economics 86:258–273.

Grimm, N. B., et al. 2008. Global change and the ecology of cities. Science 319:756–760.

Grinder, M. I., and P. R. Krausman. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. Journal of Wildlife Management 65:887–898.

Herrera, E. A., and D. W. Macdonald. 1989. Resource utilization and territoriality in group-living capybaras (*Hydrochoerus hydrochaeris*). The Journal of Animal Ecology 58:667–679.

Huijser, M. P., F. D. Abra, and J. W. Duffield. 2013. Mammal road mortality and cost–benefit analyses of mitigation measures aimed at reducing collisions with capybara (*Hydrochoerus hydrochaeris*) in São Paulo State, Brazil. Oecologia Australis 17:129–146.

Kark, S., A. Iwaniuk, A. Schalimtzek, and E. Banker. 2007. Living in the city: can anyone become an 'urban exploiter'? Journal of Biogeography 34:638–651.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82:2–27.

Lord, R. D. 1991. Twenty-four-hour activity and coprophagy by capybaras (*Hydrochaeris hydrochaeris*). Studies on Neotropical Fauna and Environment 26:113–120.

Luniak, M. 2004. Synurbization—adaptation of animal wildlife to urban development. Pp. 50–55 in Proceedings of the 4th International Symposium Urban Wildlife Conservation, Warszawa, Poland, 1–5 May 1999 (W. W. Shaw, L. K. Harris, and L. Vandruff, eds.). University of Arizona, Tucson.

MacDonald, D. W. 1981. Dwindling resources and the social behaviour of capybaras, (*Hydrochoerus hydrochaeris*) (Mammalia). Journal of Zoology 194:371–391.

Manly, B. F. L., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2007. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Marchini, S., and P. G. Crawshaw, Jr. 2015. Human–wildlife conflicts in Brazil: a fast growing issue. Human Dimensions of Wildlife 20:323–328.

Martin, J., M. Basille, B. Van Moorter, J. Kindberg, D. Allaine, and J. E. Swenson. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). Canadian Journal of Zoology 88:875–883.

Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. Worldwide urbanization and its effects on birds. Pp. 19–47 in Avian ecology and conservation in an urbanizing world (J. M. Marzluff, ed.). Springer, Boston, Massachusetts.

McDonald, R. I., P. Kareiva, and R. T. Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141:1695–1703.

Meager, J. J., T. A. Schlacher, and T. Nielsen. 2012. Humans alter habitat selection of birds on ocean-exposed sandy beaches. Diversity and Distributions 18:294–306.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. The American Midland Naturalist 37:223–249.

Mones, A., and J. Ojasti. 1986. *Hydrochoerus hydrochaeris*. Mammalian Species 264:1–7.

Moreira, J. R., K. M. P. Ferraz, E. A. Herrera, and D. W. MacDonald (eds.). 2012. Capybara: biology, use and conservation of an exceptional Neotropical species. Springer, New York.

Moreira, J. R., and D. W. MacDonald. 1997. Técnicas de manejo de capivaras e outros grandes roedores na Amazônia. Pp. 186–213 in Manejo e conservação de vida silvestre no Brasil (C. Valladares-Pádua, R. E. Bodmer, and L. Cullen, Jr., eds.). Sociedade Civil Mamirauá, Belém, Brazil.

Moreira, J. R., P. R. S. Pinha, and H. J. Cunha. 2001. Capivaras do Lago Paranoá—capybaras of the Paranoa Lake. Pp. 141–147 in Olhares sobre o Lago Paranoá (F. O. Fonseca, ed.). Secretaria de Meio Ambiente e Recursos Hídricos, Brasilia, Brazil.

Mueller, T., et al. 2011. How landscape dynamics link individual-to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography 20:683–694.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Norton, B. A., A. M. Coutts, S. J. Livesley, R. J. Harris, A. M. Hunter, and N. S. Williams. 2015. Planning for cooler cities: a framework to prioritise green infrastructure to mitigate high temperatures in urban landscapes. Landscape and Urban Planning 134:127–138.

Ojasti, J. 1973. Estudio biológico del chigüire o capibara. Fondo Nacional de Investigaciones Agropecuarias, Caracas, Venezuela.

Oliveira-Santos, L. G. R., J. D. Forester, U. Piovezan, W. M. Tomas, and F. A. Fernandez. 2016. Incorporating animal spatial memory in step selection functions. Journal of Animal Ecology 85:516–524.

Paglia, A. P., et al. 2012. Lista Anotada dos Mamíferos do Brasil/Annotated checklist of Brazilian mammals. 2nd ed. Occasional Papers in Conservation Biology No. 6. Conservation International, Arlington, Virginia.

Pozer, C. G., and F. Nogueira. 2004. Flooded native pastures of the northern region of the Pantanal of Mato Grosso: biomass and primary productivity variations. Brazilian Journal of Biology 64:859–866.

Presley, S. J., M. R. Willig, I. Castro-Arellano, and S. C. Weaver. 2009. Effects of habitat conversion on temporal activity patterns of phyllostomid bats in lowland Amazonian rain forest. Journal of Mammalogy 90:210–221.

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/. Accessed 7 February 2021.

Rengger, J. R. 1830. Naturgeschichte der saeugethiere von Paraguay. Schweighauser, Basel, Switzerland.

Sakai, R. K., et al. 2014. Experimental infection with *Rickettsia rickettsii* in an *Amblyomma dubitatum* tick colony, naturally infected by *Rickettsia bellii*. Ticks and Tick-Borne Diseases 5:917–923.

Schaller, G. B., and J. M. C. Vasconcelos. 1978. Jaguar predation on capybaras. Zeitschrift für Säugetierkunde 43:296–301.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Stolnitz, G. J. 2008. The demographic transition: from high to low birth rates and death rates. Pp. 30–46 in Population growth: the vital evolution (R. Freedman, ed.). Routledge, New York.

Therneau, T. M., and T. Lumley. 2014. Package 'survival'. Survival analysis. The Comprehensive R Archive Network. https://cran.r-project.org/web/packages/survival/index.html. Accessed 7 February 2021.

Tucker, M. A., et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359:466–469.

Verdade, L. M., and K. M. Ferraz. 2006. Capybaras in an anthropogenic habitat in Southeastern Brazil. Brazilian Journal of Biology 66:371–378.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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