Spatiotemporal dynamics of conspecific movement explain a solitary carnivore's space use

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Abstract

Patterns of space use by an individual emerge as a result of their movements, and their decisions of when and where to move are related to the distribution of resources needed for their survival and reproduction. Solitary species are characterized by limited social interaction with conspecifics, moving independently or maintaining a spatiotemporal avoidance of them, except during courtship or parental care. The present study aimed to analyze the effect of various factors on space use by jaguars (*Panthera onca*) in the Pantanal of Brazil. We used step selection functions (SSF) to evaluate the effect of the tendency to return to the home-range center (HRC), habitat, time of day and distance to conspecifics on jaguars' space use. Five jaguars with partially overlapping home ranges were simultaneously monitored using global positioning system collars. The results indicate that the main factors guiding individual movement are the spatiotemporal movements of conspecifics, differences in HRC between sexes, and the variations in habitat type throughout the day. Tracked females presented strong HRC, limiting their movements to the vicinity of their HRC, while the single tracked male did not. The habitat varies throughout the day, according to daily activities; forest and water bodies were selected all day long, but especially at night, when the species is more active and hunting. Tracked male and females selected areas that maximized the likelihood of encountering a female, but females avoided areas with a likelihood of encountering the single tracked male. Our findings allowed us to propose the solitary species' space use, highlighting the relevance of including conspecifics as factors in the selection or avoidance of determined areas.

Introduction

Patterns of animal space use are driven by different ecological and social factors, such as resource abundance and the quality and stability of different habitats, that influence animals' social-spatial organization (Mitchell & Powell, 2012; Macdonald & Johnson, 2015). Most animals move preferentially in familiar areas, restricting their movements within defined areas (Giuggioli, Potts & Harris, 2011; Potts & Lewis, 2014). To assess this movement behavior, some studies analyze movements toward the centroid of a home range (Moorcroft & Lewis, 2006; Börger & Fryxell, 2012; Flanagan et al., 2016). The selection of familiar areas provides the evidence of an individual's cognitive capacity and spatial memory (Oliveira-Santos et al., 2016), which enhance its effectiveness in finding resources by habitat selection (Forester, Im & Rathouz, 2009; Thurfjell, Ciuti & Boyce, 2014; Oliveira-Santos et al., 2016)

throughout the day (Forester et al., 2009) or by using their spatial memory of the distribution of conspecifics to avoid conflicts.

Perception of conspecifics in the environment is mediated through olfactory or visible markings that serve as cues communicating an animal's presence (Giuggioli et al., 2011; Vogt et al., 2014) and is a result of positive feedback from an increased rate of movement during the period in which an individual's scent marks remain active and renewed (Giuggioli et al., 2011; Vogt et al., 2014). Marking behavior has been observed in felines and is associated with intrasexual and intersexual communication (Vogt et al., 2014). The perception of conspecific presence may not be accurate; thus the probability of encountering conspecifics can be correlated based on their utilization distribution (UD), that is, the mechanism of conspecific perception is mediated by accumulation of the conspecifics' cues left in the environment that remains active

when they move. However, the movement depends on an individual's proximity to conspecifics. In response to the conspecifics' exact positions, the individual can move either toward, away from or independently of them over time (del Mar Delgado *et al.*, 2014).

Many carnivores are classified as territorial (Moorcroft, Lewis & Crabtree, 2006; Tallents *et al.*, 2012; Leuchtenberger, Magnusson & Mourão, 2015), with both infanticide (Soares *et al.*, 2006) and cannibalism (Azevedo *et al.*, 2010) being reported for males. However, some solitary carnivores appear to have a degree of tolerance for conspecifics (Cavalcanti & Gese, 2009; Quaglietta *et al.*, 2014; Rodgers *et al.*, 2015), sharing the same space in situations of high resource availability, with little cost to each other (Lührs & Kappeler, 2013; Elbroch *et al.*, 2016; Macdonald & Johnson, 2015). Thus, the dispersion and renewal rate of resources can determine the movement responses between individuals, influencing their spacing patterns and observed tolerance (e.g., land-tenure or resource dispersion hypothesis; see Elbroch *et al.*, 2016 and Macdonald & Johnson, 2015).

Moreover, space use in solitary species seems to differ between sexes (Lührs & Kappeler, 2013; Elbroch *et al.*, 2016; Macdonald & Johnson, 2015). Depending on the distribution of different resources, the intra- and intersexual socio-spatial organization can change. For females, spatial distribution is primarily explained by food availability, while for males, it is explained by the spatiotemporal distribution of receptive females (Ostfeld, 1990; Dammhahn & Kappeler, 2009; Giuggioli *et al.*, 2011; Lührs & Kappeler, 2013). Thus, animals' space use results from their mutual response to availability and distribution of resources and to their conspecific interactions. The influence of several conspecifics on individual movement has never before been assessed for jaguars using a dataset of simultaneously tracked conspecifics with potential for interaction.

Therefore, we investigate the movement of five jaguars, focusing mainly on conspecific influences. For this, we incorporate factors often assumed to be the large mammals' movement: (1) the movement behavior restricted by a tendency to return to the home-range center (HRC); (2) habitat type; (3) movement between different habitats throughout the day, based on daily activity pattern; (4) presence of conspecific; and (5) the sexual differences in (1), (2), (3) and (4).

Materials and methods

Study area and habitat characterization

We carried out our study in the Caiman Ecological Refuge and surrounding area, in Miranda, Mato Grosso do Sul, Brazil (19°57′02″ S, 56°18′14″ W). The area is part of the Pantanal wetland, and its vegetation is characterized by a mosaic of floodable grasslands, *cerrado*, semideciduous forest, swamps and floating vegetation (Pott *et al.*, 2011). The rainy season extends from October to April, but the flooding period depends on the declivity of the land and on the average annual evaporation, which peaks in August (Gonçalves, Mercadante & Santos, 2011). We classified the habitat types in the programs ArcGIS 10.1 (Environmental Systems Research Institute –

ESRI, 2012) and GRASS GIS 6.4 (Geographic Resources Analysis Support System – GRASS, 2012); the habitats and mapping are presented in Supporting Information Fig. S1.

Jaguar captures and GPS tracking

The Onçafari Project and the National Center for Research and Conservation of Carnivorous Mammals (CENAP-ICMBio) captured jaguars, using a soft-hold foot-snare (Frank, Simpson & Woodroffe, 2003) and following the protocol described in Morato *et al.*, 2001 for free-living jaguars. Our capture protocol was approved by the Brazilian Environmental Agency (ICMBio/SISBio License number 30053) and was consistent with guidelines outlined by the American Society of Mammalogists (Sikes, Gannon & the Animal care and use committee of the American Society of Mammalogists, 2011). We attached global positioning system (GPS) collars (Lotek Wireless) in nine individuals (three males and six females), who were then tracked between October 2011 and May 2015. Because the fixed rate transmission of the locations differed among the tracked individuals (Supporting Information Appendix S2), all nine jaguar trajectories were sampled every 2 hours to equalize the fix rate. We obtained 19 910 locations, ranging from 198 to 6373 points per individual. All the location data from the individuals were used to estimate the home range and core areas. For the step selection function (SSF) models, which required simultaneous data, we used 17 850 locations of 2-h steps recorded for five jaguars (one male and four females) tracked between October 2013 and January 2014 (more details in Supporting Information Appendix S2). At the end of the field work, we removed the GPS collars by a drop-off mechanism.

Jaguar movements

Daily activity patterns, home-range estimates and overlap

Daily activity patterns were defined by the average step length (distance between successive locations) per hour for nine jaguars. Individual patterns were defined by the average step length per hour for each individual. We used the Brownian Bridge Kernel estimator (BBK; Benhamou & Cornélis, 2010) under the isopleth probability of 95 and 50% to estimate the home ranges (km²) and core areas (km²), respectively. We used the population mean of h to calculate the minimum smoothing parameter, and the function *BRB.likD* to estimate the diffusion parameter (Benhamou & Cornélis, 2010). The home ranges and overlapping areas were estimated using the packages *adehabitatHR* (Calenge, 2006) and *Rgeos* (Bivand *et al.*, 2016) in R software (R Development Core Team 2012).

Step selection modeling

To model space use, we used SSF (see Forester *et al.*, 2009) to evaluate the influence of HRC, habitat, time of day and distance of conspecifics (male and female) on the jaguars' space use. This method considers the variation in resource availability across space relative to the current location of an individual (Thurfjell *et al.*, 2014). We generated 50 random steps

originating from the starting location of each individual step. These sets of random steps were generated based on random samples of each individual's observed distribution of step lengths (distance between successive locations) and turning angles (changes of direction between steps).

For all SSF models, we restricted our dataset to only those female and male individuals who were GPS-tracked simultaneously and whose home ranges overlapped to some extent. This restriction allowed the simultaneous calculation of the shortest male–female (M–F; indicating the influence of presence of the nearest female on the male's movement), female–male (F–M; indicating the influence of the presence of the male on movement of the focal female) and female–female (F–F) distances between individuals with a real probability of encountering each other (overlapping home ranges). Since we had no simultaneously tracked pairs of males in our dataset, we were not able to test the effect of a conspecific male on the male's movement (M–M).

Measures of HRC

We measured the distance to HRC after every movement step taken by each focal individual, for both the random steps and the observed steps (Fig. 1a). We used this measurement in the statistical model (topic below) of space use. The minimum HRC distance – selection strength $(S) > 0$ – reflects the selection of the HRC consistently over time; the maximum distance implies movement away from HRC $(S < 0)$; and when $S = 0$, individuals use areas at varying distance from the HRC according to the availability of habitats.

Measures of habitat type and time of day

For each end point of the observed and random steps, we recorded the habitat type and hour of day. The time of day was included in the model HAB*TIME (habitat time) using four harmonics ($c1_{ij}$, $c2_{ij}$, $s1_{ij}$, $s2_{ij}$) for each step i from individual j to allow a nonlinear relationship between time of day and selection strength (Forester *et al.*, 2009; Oliveira-Santos *et al.*, 2016):

$$c1_{ij} = \cos\left(\frac{\text{decimal hour}_{ij} \times 2\pi}{24}\right)$$

$$c2_{ij} = \cos\left(\frac{\text{decimal hour}_{ij} \times 4\pi}{24}\right)$$

$$s1_{ij} = \sin\left(\frac{\text{decimal hour}_{ij} \times 2\pi}{24}\right)$$

$$s2_{ij} = \sin\left(\frac{\text{decimal hour}_{ij} \times 4\pi}{24}\right)$$

Therefore, the interaction term HAB * TIME * SEX. was modeled in a linear form, as follows:

$$\text{HAB} * \text{SEX} * c1 + \text{HAB} * \text{SEX} * c2 + \text{HAB} * \text{SEX} * s1 + \text{HAB} * \text{SEX} * s2$$

In the model HAB*TIME*SEX, selection strength varies by time of day and by sex, with selection strength >0 indicating selection of the habitat type, $S < 0$ indicating an avoidance of
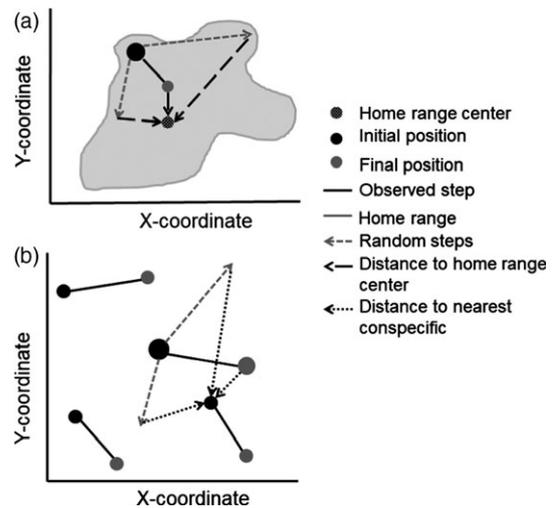

Figure 1 (a) Schema showing how we measured the home-range center distance and nearest distance to conspecifics by each step. Large circles depict the focal individual, and small circles depict the conspecifics – in example (b), three individuals – moving in the landscape. Black circles indicate the starting location (time t_0), and gray circles indicate the final location of the tracked individual (time t_2). Solid black lines represent the steps taken, gray dashed arrows indicate random steps of the focal individual (in this example, two random steps) and dashed black arrows and dotted black arrows indicate the measured distances of the observed steps and random steps of the focal individual. Adapted from Delgado *et al.* (2014).

that habitat, and $S = 0$, the use of the habitat according to availability at a given time of day.

Measures of perception and proximity to conspecific

We built two theoretical models in which individuals may perceive one another: (1) a model where the individual has no accurate information about the current position of its conspecifics and must therefore response to the accumulated spatial cues left by them (CONS-cues) (Giuggioli *et al.*, 2011; Vogt *et al.*, 2014); and (2) a model where the individual is omniscient about the current positions of its conspecifics and must therefore respond to their exact positions (CONS-omni) (del Mar Delgado *et al.*, 2014). With these two opposing models, we aimed to describe the temporal resolution of the perception of information about conspecifics' spatial location in the environment.

The first approach (1) assumes that focal individuals have a coarse perception of the distribution of conspecifics based on their spatial memory, and that movement decisions are made according to the cues that conspecifics leave throughout the landscape. In this approach, we first estimated two Kernel Brownian Bridge areas: one using all six tracked female locations (cue of females) and another using all male locations (cue of males). Because these areas are depicted by UD probability rasters that range from zero to one (lowest to highest probability of use), we recorded the UD values (from female

and male cues) for each observed step and each random step. In our case, these UD rasters represent focal individuals whose spatial distribution is influenced by potential cues (e.g., marks, feces and urine) that conspecifics leave when moving in the environment (Giuggioli *et al.*, 2011). The UD raster should identify the areas of high and low likelihood of intraspecific encounters as individuals opt either to move toward or to avoid encounters with conspecifics.

The second approach (2), following del Mar Delgado *et al.* (2014), assumes that movement decisions of focal individuals are based on the locations of conspecifics at time t_0, and that the distance in relation to their conspecifics at time t_1 would represent the decisive responses of attraction or repulsion at time t_0. Therefore, we measured a focal individual's observed distance to a conspecific after the individual had moved one step (time t_1), and we also measured the distances of the individual's random steps in relation to the locations of the nearest male and female at time t_0 (Fig. 1b). An alternative parameterization for this model is to measure the difference in distance to conspecifics at t_0 and t_1 to discern whether the individuals are approaching or moving away from their conspecifics. However, these values are strongly correlated with the values calculated using Delgado's approach (Pearson correlation $r = 0.75$), in which individuals that are approaching their conspecifics are, in most cases, closer to them at the end of the step. A value of selection strength equal to zero can be interpreted as the focal individual moving independently of conspecifics; $S > 0$ when the focal individual is attracted by the conspecific, moving closer over time; whereas $S < 0$ indicates that the focal individual avoids the conspecific, moving away over time.

Statistical models

We used conditional logistic regression (CLR) to fit the SSF (function *coxph* from the package *Survival*; Therneau & Lumley, 2015) in R statistical software (R Development Core Team 2012). This approach expresses, in exponential form, the probability of moving from place p to place P given a domain of availability D and covariates Z:

$$\Pr(\text{case} = P|D, p, Z) = \frac{\exp(\mathbf{Z}(P)\prime\boldsymbol{\beta})}{\sum_{l \in S} \exp(\mathbf{Z}(l)\prime\boldsymbol{\beta})}$$

where $\boldsymbol{\beta}$ depicts a vector of coefficients describing the strength of selection for the set of covariates represented by $\mathbf{Z}$. The CLR was conditioned to each step of each individual (observed steps = 1, random steps = 0). We controlled the

autocorrelation between successive steps of individuals by calculating robust standard errors and adjusted 95% confidence intervals (95% CI) for the coefficients estimated in the CLR (see details in Forester *et al.*, 2009).

We evaluated the space use in three phases to select the best model. We began with a model of space use that assumed the jaguar would return to its HRC. We then used this model as the foundation, based on range residency of jaguars (see Supporting Information Appendix S2 and Morato *et al.*, 2016), for a set of candidate models of space use that incorporated the effects of the following factors: habitat, daily activity, presence of conspecifics (summarized in Table 1) and all of these factors evaluated for sexual differences.

In the first phase, we evaluated sex-specific effects of HRC (interaction term HRC*SEX). The structure of the best ranked model in phase 1 by Akaike Information Criterion (AIC), was kept in phase 2. In phase 2, we evaluated the importance of habitat (HAB) and its sexual differences (interaction term HAB*SEX); the structure of the best model in this phase was kept in phase 3. Finally, in phase 3, we evaluated the effects of habitat type throughout the day (interaction term HAB*-TIME; here the model could be HAB*SEX or HAB*SEX*-TIME, depending the best model in phase 2) and assessed the influence of conspecifics on the jaguars' movements, which we measured as distance to the nearest conspecific (CONS-omni) and as density of conspecific cues (CONS-cues). We also let the effect of conspecific proximity differ according to whether the nearest conspecific was male or female (interaction term CONS-omni*SEX), and let the effect of static density of conspecific cues vary between sexes (CONS-cues*SEX). We then used the AIC (Burnham & Anderson, 2002) to compare the plausibility of the nine competing models of jaguar movement.

The full SSF model describing the selection strength can be stated in a linear form (i.e., $\mathbf{Z}(C)\prime\boldsymbol{\beta}$):

$$S = \text{HRC} * \text{SEX} + \text{HAB} * \text{SEX} * \text{TIME} + \text{CONS} * \text{SEX}$$

Camera trap information

Finally, we compiled the camera trap information for the corresponding GPS tracking period to verify the spatiotemporal presence of uncollared conspecifics (see Supporting Information Appendix S2 for details about camera trapping design). We recognized the jaguar individuals in the photographic records by their rosette patterns, and we determined their sex using a database (created in 2001) of the systematic monitoring

Table 1 Conceptual approach to sequential generation of the competitive models. The models were built with increasing complexity

Phase 1 models	Phase 2 models	Phase 3 models
Selection ~ Home-range center	Selection ~ Phase 1	Selection ~ Phase 2
Selection ~ Home-range center * Sex	Selection ~ Phase 1 + Habitat	Selection ~ Phase 2 * Time
	Selection ~ Phase 1 + Habitat * Sex	Selection ~ Phase 2 * Time + Conspecifics-Omni
		Selection ~ Phase 2 * Time+Conspecifics-Omini * Sex
		Selection ~ Phase 2 * Time + Conspecifics-Cues
		Selection ~ Phase 2 * Time + Conspecifics-Cues * Sex

of jaguar populations by other studies that involved jaguars captured by CENAP-ICMBio and Onçafari Project.

Results

Jaguar movements

Daily activity patterns, home-range area and overlap

The jaguars increased their distance traveled at crepuscular hours and at night and reduced their movement during the daylight hours (Fig. 2a). The longest average step length was 0.7 km at around 19:00, and the shortest was less than 0.2 km between 08:00 and 15:00 (Fig. 2a). Supporting Information Appendix S2 presents descriptions of home-range area, core area and overlap.

Evaluation of the space use

Step selection function model ranking indicated that despite the short period of simultaneous tracking, the models that incorporated the movement of conspecifics performed much better than the models without it (Fig. 3, Table 2). The two models in which the individuals had a finer perception of the position of conspecifics (CONS-omni; Table 2; the combined wAIC of both models was approximately 1) received much more support than the two based on distribution of cues (CONS-cues). The two best models also included the effects of HRC differentiated by sex and the habitat varying throughout the day. Coefficient estimates and 95% confidence intervals for all SSF models are available in Supporting Information Appendix S3.

According to the best model (wAIC = 0.81), the monitored females presented strong HRC, selecting areas nearest their HRC, while the single male selected areas irrespective of their distance from his HRC (Fig. 2b). Using wet grasslands as reference habitat, forest was selected through the day, particularly at night (with 1.44S at 03:00 and 0.38S at 13:00), and water bodies were selected during most of the day, except between 17:00 and 22:00. Dry grasslands were avoided in the morning and around midday (04:00–13:00), but were used at night according to their availability (maximum of 0.46S at 16:00) (Fig. 2c).

The male and females moved to maximize the chance of encountering other monitored females, selecting distances shorter than 4500 m to the nearest monitored female; the selection strength increased as distance approached zero meters. Conversely, both the male and females avoided moving more than 4500 m away from the nearest monitored female. However, the females also avoided areas with high likelihood of encountering the male, selecting distances greater than 4500 m away from him (Fig. 2d). An animation showing the spatiotemporal movement dynamics of simultaneously tracked jaguars, and an interactive graphic of distances to the nearest conspecific can be viewed at: www.leec.eco.br/data/kanda_etal_jaguar_mov.html. This animation illustrates the encounters between M1 and F2 and between F3 and F4.

Camera trap information

During the simultaneous GPS tracking of jaguars, the camera traps recorded four uncollared individuals in an area of 27.4 km² (two adult females – F5 and F7, one adult male – M4, and another adult whose sex is unknown; Supporting Information Appendix S2). We also have photographic records of cubs in the care of two (F1 and F2) of the four simultaneously tracked females during that period (Supporting Information Appendix S2). Three other females (F3, F5 and F7) were recorded with small cubs a few months before the simultaneous tracking period. Nevertheless, despite no simultaneous records of F3, F5 and F7 with cubs during the tracking period, we believe, based on visual monitoring of these individuals by Onçafari Project, that all of them were probably nursing during that time.

Discussion

Although we simultaneously monitored only five individuals in the study area, and for only a short period, our results show that SSF models that incorporate the spatiotemporal dynamics of conspecific movement in space use perform better than the models based on HRC differing between sexes and on habitat varying throughout the day. Monitored jaguar females moved in proximity to their HRC, but the single tracked male did not exhibit such behavior. This result may be related to different determinants of spatial organization according to sex (Lührs & Kappeler, 2013; Elbroch *et al.*, 2016; Macdonald & Johnson, 2015). The females' tendency to move preferentially in familiar areas may be related to their reproductive success (Piper, 2011), since most females had cubs, ranging from 8 to 17 months, in their care during the tracking period (see more in Supporting Information Appendix S2). Jaguar cubs tend to follow their mother for approximately 2 months and may remain with her for 1.5–2 years (Seymour, 1989). The females' tolerance for each other, and their tendency to return to the HRC may also be due to the combination of abundance and even distribution of food resources (de Azevedo & Murray, 2007). However, we cannot discount the possibility that these findings are artifacts of the short simultaneous monitoring period, during which the females were temporary bound to specific locations where they left the cubs.

The spatial location of monitored females seems to determine the male's use of space, which is characterized by a disinclination to remain near the HRC and a tendency to maximize his proximity to females. In small mammal populations with a high density of females, males defend territories encompassing the home ranges of several females with whom they mate polygynous (Ostfeld, 1990). Although a high density of jaguars was recorded in a nearby area in 2003–2004 (around 6.6 jaguars/100 km²) (Soisalo & Cavalcanti, 2006), we record in our short study period only six females, two males and one sex-undetermined. These findings corroborate the idea that the overall spatial organization of males may be related to a defense of females (Ostfeld, 1990; Elbroch *et al.*, 2016), rather than to prey abundance and distribution (Maletzke *et al.*, 2014). But, since solitary carnivores are defined as territorial
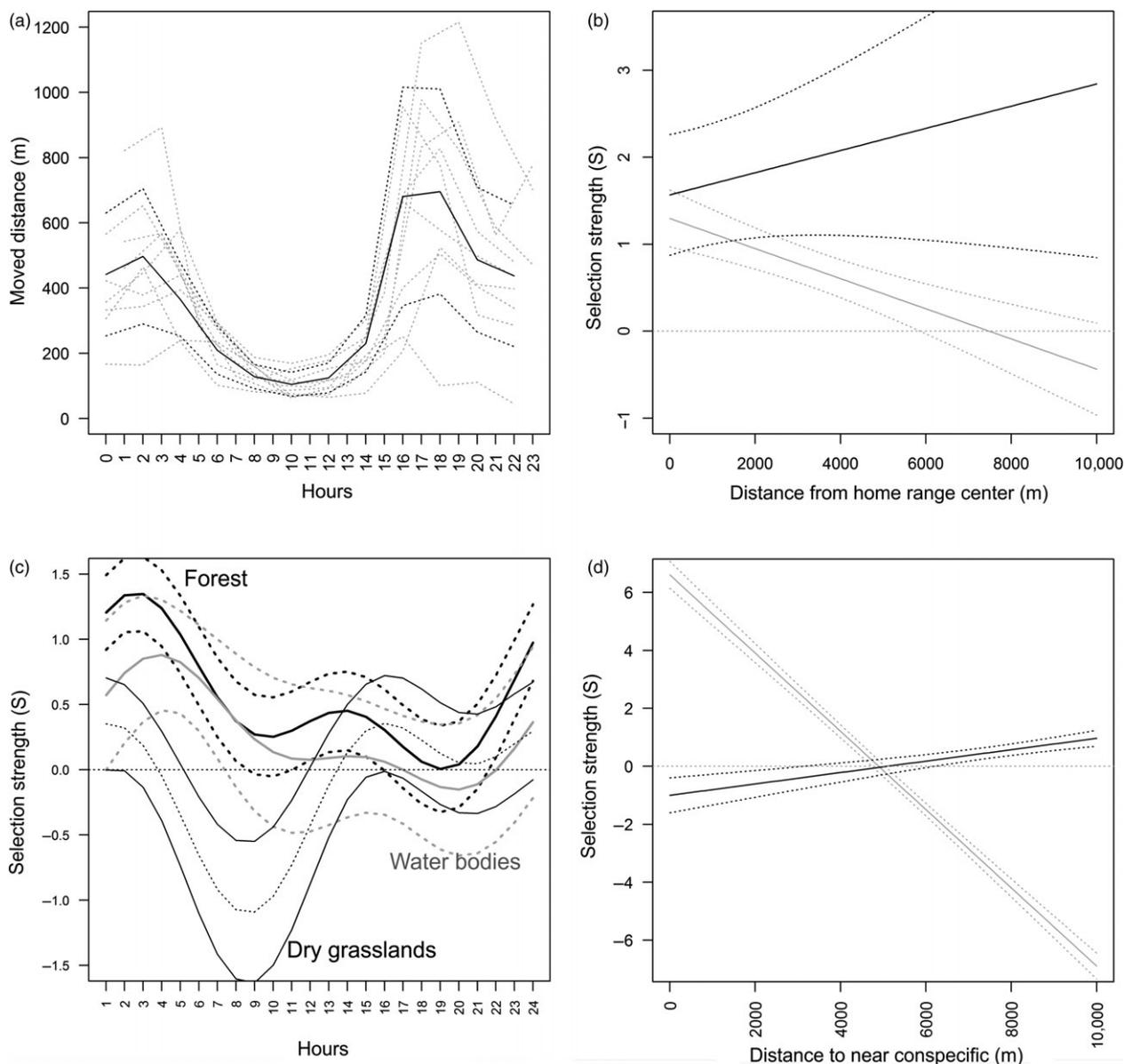
Figure 2 Effects of possible factors on jaguars' movement, based on the best ranked model and daily activity patterns. (a) In black, the mean distance moved (*m*) throughout the day. Each dashed gray line depicts one observed individual. (b) Selection strength in relation to distance (*m*) from the home-range center for males (solid black line) and females (solid gray line), and 95% confidence interval of the estimates (dotted lines). (c) Habitat selection strength throughout the day. Forest, water bodies and dry grassland are represented by the solid black line, solid gray line and dotted gray line, respectively, and the dotted line is the 95% confidence interval. (d) Selection strength in relation to the distance to the nearest conspecific (*m*). Solid gray line indicates the effect between females (F–F) and between a male and female (M–F). Solid black line represents the nearest relationship between a female and a male (F–M).

(Moorcroft *et al.*, 2006; Tallents *et al.*, 2012; Leuchtenberger *et al.*, 2015), the male, as well as the females, may be avoiding confrontation with other (untracked) males and, thus, end up using the same areas as the tracked females. To understand their influence on inter- and intrasexual movement behavior, more males need to be simultaneous tracked on a large spatiotemporal scale.

The estimated birth dates of the cubs in this study, and in Cavalcanti & Gese (2009), indicate that females have no definite period for reproduction and would be receptive at various times throughout the year. When the receptive periods of female primates are not synchronized, male monopolization is much greater than when females have synchronized receptivity (Kappeler & van Schaik, 2001). For jaguars, however, further investigation is necessary to understand the influence of the females' spatial distribution on males, especially in light of our photographic record of another male and an individual of undetermined sex in proximity to the simultaneously tracked individuals.
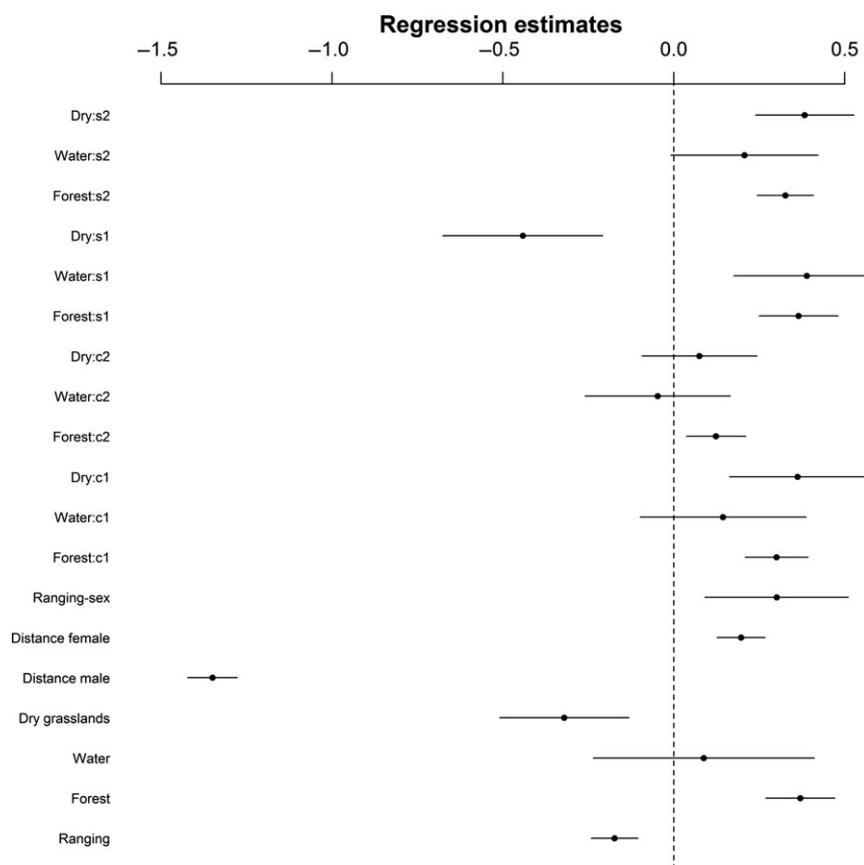
Figure 3 Conditional logistic regression parameters estimated for the best ranked SSF model (HRC * SEX + HAB * TIME + CONS-omni) (Table 2). Dots depict the parameter estimates of the model, and solid lines depict lower and upper 95% confidence intervals. The c1, c2, s1 and s2 are harmonics used to include the interaction term between habitat type and time of day.

Table 2 Model ranking of the seven competitive SSF models

Models	LogLikelihood	k	AIC	wAIC	ΔAIC
HRC * SEX + HAB * TIME + CONS-omni	−37 092.51	19	74 223.03	0.81	0
HRC * SEX + HAB * TIME + CONS-omni * SEX	−37 091.57	20	74 225.13	0.18	2.10
HRC * SEX + HAB * TIME + CONS-cues	−43 263.39	19	86 570.36	<0.01	12 353.44
HRC * SEX + HAB * TIME + CONS-cues * SEX	−43 266.18	20	86 566.79	<0.01	12 357.01
HRC * SEX + HAB * TIME	−43 396.33	17	86 826.67	<0.01	12 603.64
HRC * SEX + HAB	−43 498.09	5	87 006.17	<0.01	12 783.14
HRC * SEX + HAB * SEX	−43 495.44	8	87 006.89	<0.01	12 783.85
HRC * SEX	−43 585.94	2	87 175.88	<0.01	12 952.85
HRC	−43 586.98	1	87 175.95	<0.01	12 952.93

K = number of parameters; wAIC = weight of the models; ΔAIC = difference between the AIC value of the current model and lowest AIC value. Home-range center (HRC); HRC differing between sexes (HRC*SEX); habitat (HAB); the habitat varying by time of day (HAB*TIME); distance to nearest conspecific (CONS-omni); distance to nearest conspecific with sexual variation (CONS-omni*SEX); density of cues (CONS-cues); and density of cues by sex (CONS-cues*SEX).

The monitored jaguars selected different habitats depending on the time of day, selecting forest and water during nocturnal activities and avoiding dry areas during periods of rest. Similar to reports on wild boar (Oliveira-Santos et al., 2016) and elk (Forester et al., 2009), the jaguars' habitat selection seems to be related to their daily activity patterns. The preference for forest habitats and water

appears to be common for this species in Brazil (Astete, Sollmann & Silveira, 2007), and their selection may be related to a preference for consuming prey associated with these habitats (Astete et al., 2007; Azevedo et al., 2010; Cavalcanti & Gese, 2010).

The two best models included the influence of distance to the nearest conspecific, providing support for the hypothesis that

individuals perceived each other at a fine temporal resolution (del Mar Delgado *et al.*, 2014). Felids seem to use vocalization for long-distance communication with conspecifics (Kleiman & Eisenberg, 1973), suggesting that jaguars have a long perception distance and can obtain some (coarse) information about the current position of their conspecifics; Kleiman & Eisenberg (1973) do not mention the distance at which this happens. Moreover, the second-best model contributed little new information and was not truly competitive with the best model (Arnold, 2010). Both the male and female jaguars moved toward females, selecting distances of zero meters, but females tended to avoid the single tracked male. We were unable to perform standard validation on the models' assumptions because we GPS-tracked only a few individuals simultaneously.

Moreover, our results showing the females' behavior to minimize encounters with the male may support reports of cannibalism (Azevedo *et al.*, 2010) and infanticides committed by a male jaguar (Soares *et al.*, 2006). Despite this report of infanticide, one of our study's females with cubs under her care, F2, had encounters with a male. We do not know whether that male fathered those cubs and thus tolerates their presence; however, male felids typically do not participate in parental care (Kleiman & Eisenberg, 1973). Similar sightings have been reported in the literature on jaguars in the Pantanal (Cavalcanti & Gese, 2009), and the mechanisms that prevent infanticide are still poorly understood (Soares *et al.*, 2006).

The jaguars' overall spatial organization appears to be related to the spatial distribution and availability of resources (Ostfeld, 1990; Mitchell & Powell, 2007; Elbroch *et al.*, 2016), suggesting that the heterogeneity of resources may explain variable sociality (Macdonald & Johnson, 2015), including conspecific avoidance when hunting (Bandeira De Melo *et al.*, 2007; Elbroch *et al.*, 2016) or temporal aggregations of conspecifics in areas of high resource availability (Elbroch *et al.*, 2016). Additional studies focusing on resource distribution and space organization are necessary to verify this generality.

Our study sheds new light on how the presence of conspecifics can influence patterns of movement and thus shape the way that animals use space. The findings show that even solitary carnivores possess some degree of tolerance of conspecifics. However, further research with simultaneous tracking of a larger sample of individuals is necessary, because it would allow us to more clearly identify the main mechanisms that govern animal space use, highlighting the relevance of intrasexual and intersexual conspecifics in the selection or avoidance of determined areas.

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Supporting Information

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

Appendix S1. Landscape mapping details

Appendix S2. Information about GPS tracking; home range, core area and overlapping home range and core area; camera traps distribution and; records of female jaguars with cubs.

Appendix S3. Coefficient estimates and 95% confidence intervals of the all ranked step selection function models.