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Space use and movement of jaguar (*Panthera onca*) in western Paraguay

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Abstract: Home range and core area size were estimated for jaguar (*Panthera onca*) in western Paraguay in the Dry Chaco, Humid Chaco and Pantanal using an autocorrelated kernel density estimator. Mean home range size was 818 km² (95% confidence interval: 425–1981) in the Dry Chaco and 237 km² (95% confidence interval: 90–427) in the Humid Chaco/Pantanal. Core areas, defined as the home range area where use was equal to expected use, was consistent across sexes and systems represented on average by the 59% home range isopleth (range: 56–64%). Males had a higher probability of larger home ranges and more directional and greater daily movements than females collectively and within systems. The large home ranges in the Dry Chaco are attributable to the relatively low productivity of that semi-arid ecosystem and high heterogeneity in resource distribution while larger than expected home ranges in the Humid Chaco/Pantanal compared to home range estimates from the Brazilian Pantanal may be due to differences in geomorphology and hydrological cycle. The large home ranges of jaguars in western Paraguay and a low proportional area of protected areas in the region demonstrate the importance of private ranchland for the long-term conservation of the species.

Keywords: autocorrelated kernel density estimation; Chaco; home range; jaguar; Pantanal; *Panthera onca*; Paraguay.

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Introduction

Globally, apex predators, and the maintenance of their functional roles, are severely threatened due to anthropogenic pressures, particularly associated with large spatial needs to access sufficient prey to meet metabolic requirements and persecution (Ripple et al. 2014). Habitat conversion and degradation and over hunting of prey species increase spatial requirements of apex predators, increasing conflict with humans and affecting social behavior, dispersal and habitat use (Macdonald 1983, Crooks 2002, Cardillo et al. 2004, Ripple et al. 2014). Consequently, an understanding of the space use and movement ecology of apex predators is key to effective conservation decision making for these species.

The jaguar (*Panthera onca*) is the largest feline in the Americas, distributed from the southwestern United States to northern Argentina, although it presently occupies <50% of its original range, and <80% of the range outside of Amazonia, due to habitat loss and persecution (Sanderson et al. 2002, Zeller 2007, de la Torre et al. 2017). Given the contraction of the species' distribution, range-wide conservation efforts have focused upon maintaining connectivity among key populations throughout the species' range (Sanderson et al. 2002, Rabinowitz and Zeller 2010), however, an effective implementation of this management approach is partly dependent upon a thorough understanding of the spatial and movement ecology of jaguars.

For a big cat the jaguar is relatively understudied (Brodie 2009), and although multiple studies have estimated jaguar home range size (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Crawshaw and Quigley 1991, Crawshaw 1995, Scognamillo et al. 2002, Crawshaw et al. 2004, Silveira 2004, Cullen 2006, Azevedo and Murray 2007, Cavalcanti and Gese 2009, Tobler et al. 2013, Morato et al. 2016) and movements (Conde et al. 2010, Colchero et al. 2011, Sollmann et al. 2011, Morato et al. 2016), there is still relatively little known about the species' spatial and movement ecology. Since anthropogenic factors drive jaguar occurrence throughout its range by determining habitat availability and quality (Zeller et al. 2011, Petracca et al. 2014a,b, Thompson and Martínez Martí 2015) this conspicuous knowledge gap on

how jaguars perceive and use the landscape is of concern as it limits managers' ability to quantifiably design and manage conservation landscapes for the jaguar.

Range-wide, the jaguar is considered near threatened (Quigley et al. 2017), however, at the austral limit of its distribution the species is considered critically endangered in Argentina and endangered in Brazil and Paraguay. Although multiple studies have investigated space use by jaguar in Brazil and Argentina (Schaller and Crawshaw 1980, Crawshaw and Quigley 1991, Crawshaw 1995, Crawshaw et al. 2004, Silveira 2004, Cullen 2006, Azevedo and Murray 2007, Cavalcanti and Gese 2009, Morato et al. 2016) there has been no such research on the species in Paraguay despite a recognized need in the face of a rapid constriction in the species' distribution in relation to a country-wide expansion of the agricultural sector (Secretaría del Ambiente et al. 2016) which has resulted in some of the highest rates of deforestation in the world (Hansen et al. 2013).

Given the status of the jaguar in Paraguay, the lack of information on the spatial and movement ecology of the species is of concern within the context of continued habitat loss, the maintenance of in-country and trans-boundary connectivity of populations, and their implications for the range-wide conservation of the jaguar. Consequently, GPS-based telemetry was used to study space use and movements of jaguars in western Paraguay in the Dry Chaco, Humid Chaco and Pantanal, the region with the largest jaguar population in the country. Moreover, developing methodologies were employed to determine home range residency and account for autocorrelation in the data (Fleming et al. 2014, 2015, Calabrese et al. 2016), allowing for rigorous comparisons with estimates from other research employing the same methodologies (Morato et al. 2016), which is a recognized need for jaguar spatial ecology (Gonzalez-Borrajo et al. 2017).

Based upon carnivore ecology in general, and jaguar ecology specifically, it was expected that male home range size and movement rates would be greater than those of females (Sandel 1989, Cavalcanti and Gese 2009, Conde et al. 2010, Sollmann et al. 2011, Morato et al. 2016, Gonzalez-Borrajo et al. 2017) and that jaguars in the Dry Chaco would exhibit larger home ranges, higher movement rates, and more directional movement compared to those in the more productive habitats of the Humid Chaco and Pantanal (Sandel 1989, Fahrig 2007, Gutiérrez-González et al. 2012). Also, when compared to other sites (Morato et al. 2016) it was expected that estimates from the Humid Chaco and Pantanal would be similar to those from the Brazilian Pantanal, while estimates from the Dry Chaco would be larger than those from more humid systems but possibly similar to jaguars from the Brazilian Cerrado due

to biotic and abiotic similarities between systems. Apart from constituting an important contribution towards the conservation of jaguars within Paraguay, placing the results into a comparative context with research from neighboring countries will facilitate the efficacy of trans-boundary conservation efforts, with important implications for range-wide conservation strategies for jaguar.

Materials and methods

Study area

The study was conducted in three ecosystems in western Paraguay; Dry Chaco, Humid Chaco and Pantanal (Figure 1). The Dry Chaco is comprised of xeric forest, savannas and grasslands and the Humid Chaco and Pantanal are a mosaic of seasonally flooded grasslands, palm savanna and xerophilic woodlands on higher ground (Olson et al. 2001, Mereles et al. 2013). The delineations between the Humid Chaco and Pantanal differ (Olson et al. 2001, Mereles et al. 2013), however, for this study the similarities between systems and among study sites in those systems make this discrepancy moot and consequently the Humid Chaco and Pantanal were treated as a single system in the analysis.

The western half of Paraguay is generally semi-arid with a pronounced east-west gradient in precipitation and humidity which divides the Chaco into the Humid Chaco with precipitation approximately >1000 mm/year and the Dry Chaco with precipitation <1000 mm/year (Olson et al. 2001). The Pantanal is also subjected to this east-west precipitation gradient; however, it and the Humid Chaco are also strongly affected by the hydrological cycles of the Rio Paraguay (Mereles et al. 2013).

In the Humid Chaco the study area was conducted on Estancia Aurora, a 30,000 ha cattle ranch in the north of the department of Villa Hayes and in the Pantanal on the 65,000 ha ranch Estancia Fortín Patria and on a 80,000 ha section of the ranch Estancia Leda. In the central Dry Chaco, research was undertaken on the 50,000 ha Faro Moro ranch and more northerly in the 720,000 ha Defensores del Chaco National Park and the neighboring 269,000 ha of ranchland of the former consortium *Grupo Chovoreca*.

Jaguar captures

Jaguars were captured using trained hounds to tree or bay jaguars which were then anesthetized using a

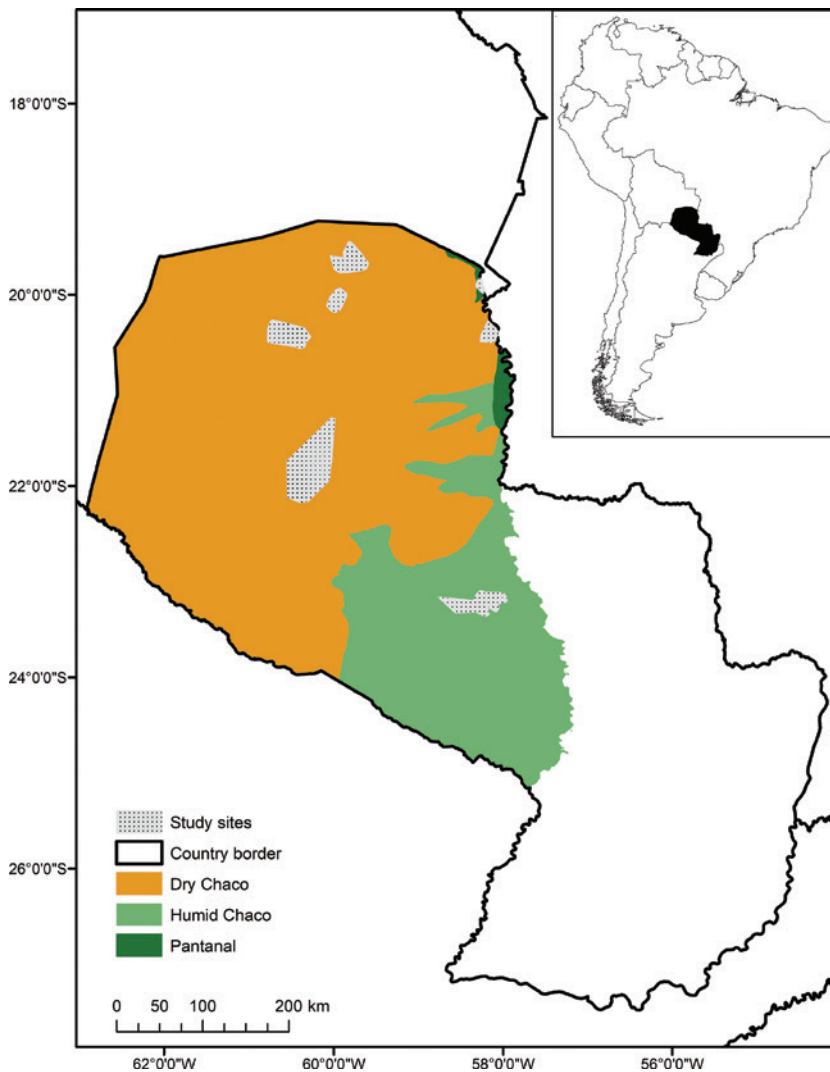


Figure 1: Map showing the location of Paraguay in South America, the distribution of the Dry and Humid Chaco and Pantanal in western Paraguay (Olson et al. 2001) and study areas where jaguar movements were monitored.

weight-dependent dose of a mix of ketamine hydrochloride and xylazine hydrochloride injected by a dart shot from a tranquilizer gun (McBride and McBride 2007). Capture methods followed American Society of Mammalogy protocols (Sikes 2016) and in >60 captures and recaptures of jaguar and puma over the study period there were no deaths or noticeable injury to animals.

From 2002 to 2009 jaguars were fitted with Telonics Generation II, data store-on-board, GPS collars (Telonics, Mesa, AZ, USA) which were set to record locations at 4 h intervals. Starting in 2009 Northstar GPS collars (D-cell, Northstar, King George, VA, USA) programmed to record locations at 4 h intervals were used and beginning in 2012 Telonics Generation III GPS collars (Telonics, Mesa, AZ, USA) were used which were set to record locations daily every 2 h from 1800 to 0600 h.

Home range estimation

To estimate home ranges continuous-time stochastic movement models were fit to the telemetry data, incorporating variogram analysis of semi-variance in locations in relation to time lags to inspect the autocorrelation structure in the data over time and to account for variable sampling intervals (Fleming et al. 2014). Starting values derived from semi-variance functions were used for maximum likelihood model fitting with model selection based upon Akaike Information Criteria, adjusted for small sample size (AICc), and model weights (Fleming et al. 2014, 2015, Calabrese et al. 2016). If the best fitting model displayed range residency by an individual the model was used to estimate a home range using autocorrelated kernel density estimation (AKDE; Fleming et al. 2015).

Movement models tested were a random search model (Brownian motion) with uncorrelated velocities and no limits to space use, a random search model with constrained space use (Ornstein–Uhlenbeck, OU), and Ornstein–Uhlenbeck motion with foraging (OUF) which is the OU process with correlated velocities (Fleming et al. 2014, Calabrese et al. 2016). All these models account for autocorrelation in positions, while the OUF model accounts for autocorrelation in velocities and the OU and OUF models include range residency (home range). Consequently, the OU and OUF models produce estimates of home range size and home range crossing time, while the OUF model additionally estimates the velocity autocorrelation time scale (a measure of path sinuosity) and mean distance traveled per day (Fleming et al. 2014, Calabrese et al. 2016).

If individuals exhibited residency in their movements home range areas were estimated using AKDE based upon the best fitting model. When applied to serially autocorrelated data AKDE more accurately estimates home range compared to traditional kernel density estimation (KDE; Worton 1989) as KDE assumes independent identically distributed data (IID), which when violated, can result in greatly underestimated home range size (Fleming et al. 2015).

Semi-variogram analysis, model selection and AKDE were undertaken using the *ctmm* package (Calabrese et al. 2016) in R 3.3.2 (R Development Core Team 2010). Data collected with an irregular sampling schedule starting in 2012 were accounted for using the *dt* argument within the *variogram* function in the *ctmm* package (Calabrese et al. 2016). Additionally, for comparison with home range estimates from previous research using traditional home range estimators, both the 95% KDE home ranges under a model assuming IID and 95% minimum convex polygons (MCP) home ranges (Burt 1943) were estimated using the *ctmm* (Calabrese et al. 2016) and *adehabitatHR* (Calenge 2006) packages in R, respectively (Supplementary Table 1).

Core area estimation

Core areas of AKDE home ranges were estimated as the area encompassed within the isopleth where the proportional use of the estimated home range is equal to the predicted probability of use (Seaman and Powell 1990, Bingham and Noon 1997, Vander Wal and Rodgers 2012). This was determined by fitting an exponential curve to the isopleths of the AKDE home range of each individual at 10% increments from 10 to 90%, and at the 95 and 99% isopleths,

in relation to the proportional area of the home range that each of those isopleths encompassed based upon the area of the 99% home range estimate. The threshold where proportional home range size begins to increase at a rate greater than the probability of use (slope = 1; Seaman and Powell 1990, Bingham and Noon 1997, Vander Wal and Rodgers 2012) was determined to define the isopleth that represented the core area boundary.

Statistical analyses

For the statistical analysis jaguars from the Humid Chaco and the Pantanal were combined into a single group since the characteristics of the system are highly similar, with the delineation between the two systems debatable (Olson et al. 2001, Mereles et al. 2013), and consequently jaguars from those systems are subjected to similar ecological and anthropogenic drivers. Additionally, only individuals that exhibited residency in their movement behavior and space use [demonstrated by their variograms reaching an asymptote at approximately their home range crossing time (Fleming et al. 2014, Calabrese et al. 2016)] were included in the comparative analysis of differences between sexes and ecosystems.

A fixed-effect one-way analysis of variance (ANOVA) in a Bayesian modeling framework was used to test for differences in estimates of home range size, home range crossing time, directionality in movement (velocity autocorrelation time scale) and mean daily distance traveled between sexes (systems combined), between systems (sexes combined), between sexes within a system, and between same sexes between systems. Normality in the data was tested using the Shapiro-Wilk test and log-transforming the data when their distribution did not meet assumptions of normality.

The analysis was undertaken in R 3.2.2. (R Development Core Team 2010) using WinBUGS (Lunn et al. 2000) and the *R2WinBUGS* package (Sturtz et al. 2005). WinBUGS was run with three chains for 100,000 iterations and a 20,000 iteration burn-in period; confirming convergence by a scale reduction factor ≤ 1.1 and visual inspection of trace plots for lack of autocorrelation (Gelman and Hill 2007). Differences between groups were tested by taking 10,000 random samples from posterior distributions for each group of interest, comparing the proportional frequency (probability, *p*) that posterior estimates of parameters were different for males than females overall and within systems, different for all individuals between systems, and different between same sexes between the Dry Chaco and the Humid Chaco/

Pantanal. The closer p is to 0 or 1 the greater the probability that the groups are different, while there is no difference between groups when $p = 0.5$.

Results

Jaguar captures and data collection

From June 2002 to June 2014 35 jaguars were captured and collared, of which 19 individuals provided sufficient data for analysis; seven in the Dry Chaco (five males, two females), nine in the Humid Chaco (three males, six females) and three in the Pantanal (one male, two females) with estimated ages between 2 and 10 years (Table 1). Collars collected data between 52 and 439 days, obtaining from 148 to 3462 locations (Table 1).

Home range, core area and movement parameter estimates

Best fitting models for the movement of jaguars were either the OU or OUF models with 16 individuals demonstrating

residency (Table 1). Estimated home range sizes varied between 86 and 2909 km² and core areas between 21 and 504 km². Core areas were represented by a consistent proportion of the home range; ranging between the 56 and 64% isopleths (Table 1).

Male and female mean home range size were 727 km² (95% confidence interval (CI): 355–1954) and 255 km² (95% CI: 90–578), respectively and 818 km² (95% CI: 425–1981) and 237 km² (95% CI: 90–427) for jaguars in the Dry Chaco and Humid Chaco/Pantanal, respectively. In the Dry Chaco mean home range size for males was 925 km² (95% CI: 424–2035) and 551 km² (95% CI: 513–590) for females, while in the Humid Chaco/Pantanal the mean home range was 398 km² (95% CI: 345–427) and 156 km² (95% CI: 90–267) for males and females, respectively (Figure 2).

Males demonstrated larger home ranges ($p = 0.99$), higher daily movement ($p = 0.84$), greater directionality in movement (velocity autocorrelation time scale) ($p = 0.84$) and lower home range crossing times ($p = 0.9$) (Table 2). Between systems, home ranges were larger ($p = 1$), movements more directional ($p = 0.99$) and home range crossing times greater ($p = 0.77$) in the Dry Chaco, while daily travel distance was similar between systems but with a slightly higher probability of being larger in the Dry Chaco ($p = 0.61$).

Table 1: Sex, age, sample characteristics and estimated movement parameters, AKDE home range, core area and core area isopleths for study jaguars in the Paraguayan Dry Chaco, Humid Chaco and Pantanal.

ID	Sex/age (year)	Number of fixes/days	Velocity autocorrelation timescale (h)	Home range crossing time (days)	Average distance traveled (km/day)	Home range (km ²) (95% CI)	Core (km ²)	Core area isopleths (%)
Dry Chaco								
DC1	M/5	1094/376	1.1	8.0	28.8	2143 (1558–2820)	504	59
DC3	M/2	722/363	1.8	11.5	7.9	421 (288–580)	107	63
DC4	M/5	620/82	1.9	3.5	15.0	550 (349–797)	182	58
DC6	M/7	1387/393	2.2	4.8	19.3	1063 (822–1335)	329	57
DC7	M/5	3462/439	1.4	2.7	17.1	445 (381–515)	85	64
DC5	F/6	1610/386	1.1	11.5	11.8	591 (411–805)	178	59
DC2	F/8	921/379	1.7	9.5	9.7	511 (363–683)	176	56
Humid Chaco/Pantanal								
Pan2	F/2	1694/375	1.1	4.3	7.9	71 (58–85)	24	60
HC5	F/4	593/242	0.5	1.2	20.9	92 (75–110)	23	61
HC4	F/3	288/266	1.5	6.2	9.3	270 (187–369)	86	57
HC8	F/1	980/170	0.2	10.2	13.7	121 (71–183)	32	58
HC7	F/6	1668/324	0.1	9.2	22.3	246 (172–332)	73	57
HC9	F/6	928/362	0.2	9.7	13.9	118 (83–159)	33	59
Pan3	M/6	727/192	1.4	3.4	16.6	428 (320–550)	134	57
HC3	M/4	983/143	1.4	4.4	15.0	424 (290–584)	138	56
HC6	M/10	660/133	0.9	5.5	13.4	341 (216–494)	91	60
Pan1	F/4	1695/366	NA	3.5	NA	550 (349–797)	21	60
HC1	M/6	148/88	NA	5.9	NA	958 (534–1505)	283	58
HC2	F/6	280/54	NA	5.7	NA	73 (35–125)	22	57

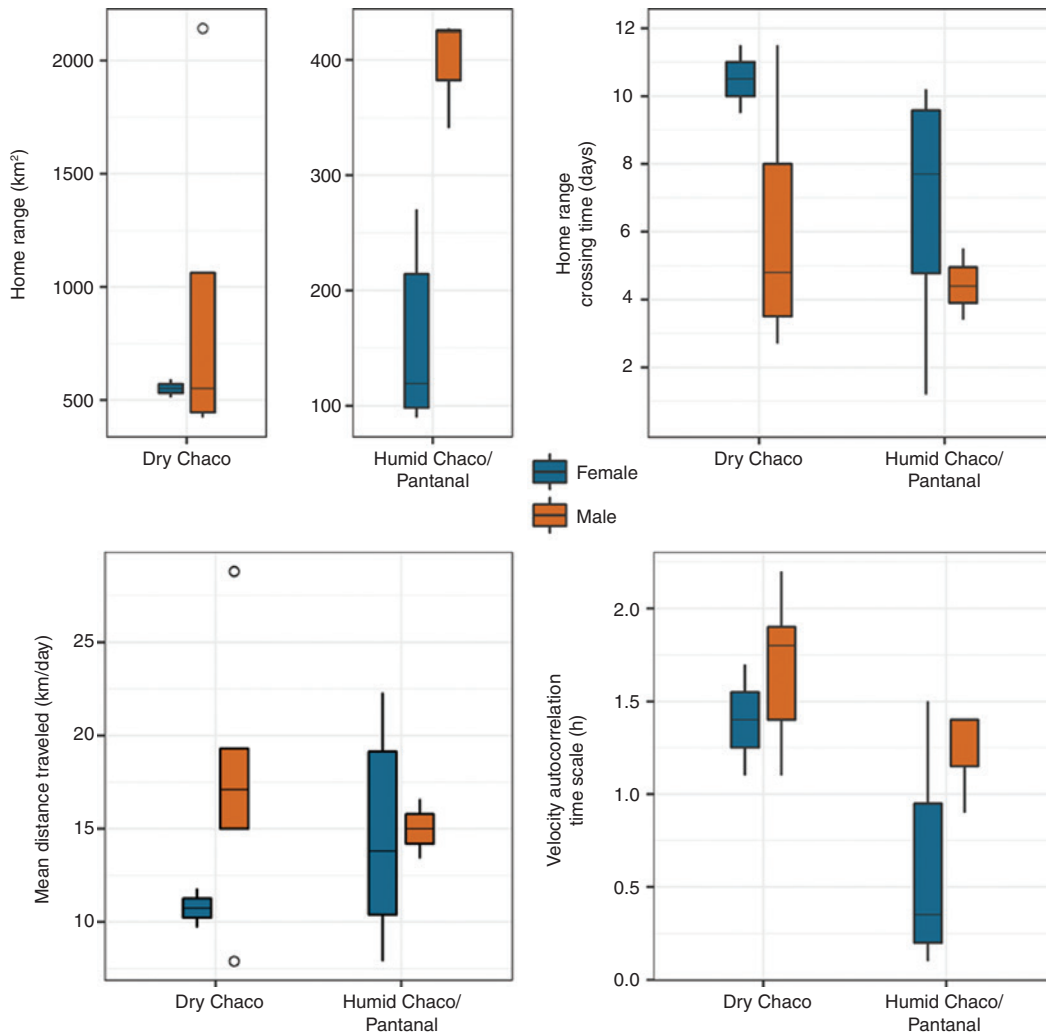


Figure 2: Home range and movement parameters of male and female jaguars in the Dry Chaco and Humid Chaco/Pantanal. Boxes show the median and 25 and 75% percentiles with whiskers representing the data range within 1.5 times the distance of the box.

Table 2: Probabilities based upon posterior distributions, that home range and movement parameters are different between sex and ecosystem, between sexes within systems, and between same sexes between systems.

	Home range (km ²)	Home range crossing time (days)	Velocity autocorrelation timescale (h)	Average distance traveled (km/day)
Dry Chaco male > Dry Chaco female	0.71	0.08	0.71	0.89
Humid Chaco/Pantanal male > Humid Chaco/Pantanal female	0.99	0.17	0.95	0.52
Dry Chaco male > Humid Chaco/Pantanal male	0.91	0.75	0.86	0.72
Dry Chaco female > Humid Chaco/Pantanal female	0.99	0.89	0.96	0.23
All Dry Chaco > All Humid Chaco/Pantanal	1	0.77	0.99	0.61
Male > Female	0.99	0.10	0.99	0.84

Between systems males in the Dry Chaco had higher probabilities to have larger home ranges ($p=0.91$), higher home range crossing time ($p=0.75$), greater directionality in movement ($p=0.86$), and greater daily travel

distances ($p=0.72$) (Table 2), although values for all parameters were more variable in males from the Dry Chaco (Figure 2). A similar pattern was evident between females in both systems for home range size ($p=0.99$), home range

crossing time ($p=0.89$) and directionality in movement ($p=0.96$) which were greater for females in the Dry Chaco, however, females in the Dry Chaco had lower daily movements ($p=0.77$) than those in the Humid Chaco/Pantanal (Table 2).

Discussion

These are the first estimates of movement parameters and home range and core area for jaguar in the Dry Chaco, Humid Chaco, and Paraguayan Pantanal, which furthermore take advantage of developing methods to empirically test for home range residency and account for autocorrelation in telemetry data when estimating space use (Fleming et al. 2014, 2015, Calabrese et al. 2016). The results include the largest home range estimates recorded for jaguar (Dry Chaco) and, as expected, jaguars in the more productive Humid Chaco/Pantanal had smaller home ranges, lower movement rates and had less directionality in movements compared to jaguars in the Dry Chaco. Also, consistent with previous research males had larger home ranges, higher movement rates and more directional movements than females overall and within systems.

Overall and between systems male home ranges were larger than females which was expected (Cavalcanti and Gese 2009, Sollmann et al. 2011, Morato et al. 2016, Gonzalez-Borrajo et al. 2017) as female home range size is driven to maximize food availability and reproductive success while minimizing metabolic costs, which consequently results in home range sizes that are at an optimal minimum (Sandel 1989, Sunquist and Sunquist 1989). Conversely, male home ranges are driven by food availability and a need to maximize contact with receptive females which leads to males maximizing home range size towards optimizing reproductive opportunities constrained by their metabolic limits (Sandel 1989, Sunquist and Sunquist 1989). This relationship is further supported by the estimated movement parameters which showed that males traveled farther, faster, and more directionally than females in response to the need to cover and maintain their larger home ranges.

Consistent with expectations home range sizes of jaguars in the Dry Chaco were larger than in the Humid Chaco and Pantanal, overall and between sexes within systems where male home ranges were greater than females. The larger home ranges in the Dry Chaco are attributable to the lower productivity of that semi-arid ecosystem, more heterogeneously distributed prey and water, and negative effects of anthropogenic factors (i.e. deforestation; Fahrig 2007, Gutiérrez-González et al. 2012).

Home range estimates from the Dry Chaco for both males and females are considerably larger than other estimates from this study and Morato et al. (2016), although estimates of male home range size from the Dry Chaco (mean: 925 km², 95% CI: 424–2035) are consistent with the estimate for a single male from the Brazilian Cerrado (1269 km²), a semi-arid ecosystem with environmental and land use similarities to the Gran Chaco. Morato et al. (2016) demonstrated that increasing home range size of jaguars was associated with lower habitat quality, which is consistent with the very large home ranges from the Dry Chaco which, although larger, were closest in size to Morato et al.'s (2016) home ranges in the Atlantic forest which they considered to be of the lowest habitat quality of their study areas.

Home range sizes from the Humid Chaco/Pantanal were expected to be similar to estimates from the Brazilian Pantanal, however, estimates were 59 and 112% larger for males and females, respectively, than home ranges reported for the Brazilian Pantanal; falling between estimates from the Amazon and Atlantic forest, although most similar to jaguars from the Amazon (Morato et al. 2016). These differences may be related to differences in the geomorphology of the two regions and its interaction with local hydrological cycles.

The Paraguayan Pantanal and the study area in the Humid Chaco have less forest area and a relatively greater area of inundated land during a large portion of the year compared to the Pantanal study areas of Morato et al. (2016) in Brazil. Consequently, the reduced forest area, with smaller and more isolated forest patches during annual flooding, could drive the comparatively larger home ranges observed in the Paraguayan Pantanal and Humid Chaco, although reduced jaguar densities resulting from persecution may also play a role in liberating available space and permitting greater space use.

Differences in the mean movement parameters were evident between jaguars in the Humid Chaco/Pantanal and in the Brazilian Pantanal whereby movements were more directional in the Humid Chaco/Pantanal, although still relatively sinuous but most similar to jaguars in the Atlantic forest, while daily movements were very similar to those in the Amazon. Jaguars in the Dry Chaco had high movement rates and directionality in movement, similar to individuals from the Amazon in seasonally flooded forests (Morato et al. 2016).

These similarities are possibly responses to movements among sporadically distributed critical resources (prey, water, mates) despite the large differences in ecosystem characteristics. Conversely, although daily movement rate of jaguars in the Humid Chaco/Pantanal were

similar to those in the Dry Chaco and Amazon, the relatively low directionality demonstrated by jaguars in the Humid Chaco/Pantanal suggests that, although jaguars are covering relatively large areas, movements are in response to more homogeneously distributed resources within home ranges.

Core area size was highly similar across systems and sexes, encompassed on average by the 59% home range isopleth (95% CI: 56–64%), which represented on average 29% (95% CI: 21–34%) of total home range area. This indicates that despite home range size, sex, or system jaguars are most intensively using about a third of their home range area. Additionally, the results suggest a cautious interpretation of arbitrarily defined core area delimitations (Powell 2012), however, it is also recognized that with AKDE home ranges the median or mean area are justifiable measures of central tendency (Fleming and Calabrese 2017).

In light of the extensive deforestation that is occurring in the Dry Chaco of western Paraguay, the large home ranges observed in this system, which are consistent with the estimated low density of jaguar in the Bolivian Dry Chaco (Noss et al. 2012), are of concern as they demonstrate the large forested area that jaguars in the Dry Chaco require. In the Humid Chaco/Pantanal spatial requirement of jaguars were greater than expected based on estimates from the Brazilian Pantanal, which suggests lower than expected densities in these systems in Paraguay and cautions against extrapolating population parameter estimates from other regions within the Pantanal to the Rio Paraguay flood plain in Paraguay.

In both the Dry Chaco and the Humid Chaco/Pantanal there may be an important effect on space use caused by reduced jaguar densities from persecution which is pervasive throughout western Paraguay, illustrated by the confirmation that >50% of the study animals were killed due to persecution. Persecution is common throughout the range of the jaguar, however, its practice and magnitude is not equivocal geographically and consequently how the removal of individuals may impact space use, and subsequently comparisons among ecosystems and regions, needs to be considered and is of interest for future research.

The large spatial requirements of jaguars in western Paraguay, particularly in the Dry Chaco, indicate that the protected areas of the region, which represent <5% of the total regional area, are likely insufficient to maintain a viable regional population, especially in light of the level of persecution on private lands. This highlights an urgent need to mitigate jaguar-human conflict in the region by actively including the livestock production sector in the

conservation decision making process. Furthermore, given continuing deforestation, conservation initiatives need to take into account the large spatial needs of jaguar in western Paraguay by recognizing and incorporating the role of private lands in the long-term conservation of the species in Paraguay and in maintaining trans-boundary connectivity among populations.

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