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## SPATIAL ECOLOGY AND SOCIAL INTERACTIONS OF JAGUARS (*PANTHERA ONCA*) IN THE SOUTHERN PANTANAL, BRAZIL

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The Pantanal of Brazil is an important area for the conservation of jaguars (*Panthera onca*). As the size of traditional large ranches in the Pantanal decreases, human access to jaguar habitat increases, resulting in human-altered landscapes that may influence patterns of resource selection and space use by jaguars. We used global positioning system radiocollars to study jaguars in the southern Pantanal. We radiocollared 10 jaguars (6 males and 4 females), obtained 11,787 locations, and examined their space use, movement rates, and social interactions between October 2001 and April 2004. Estimates of 90% kernel home ranges varied among animals and seasons (range: 34.1–262.9 km<sup>2</sup>). Core areas (50% isopleth) of both females and males did not differ in size between seasons, but home ranges (90% isopleth) during the dry season were generally larger than during the wet season. The stability of home ranges varied among seasons and individuals. Some females maintained  $\geq 80\%$  of their home ranges from 1 season to the next, whereas other females used  $\leq 50\%$  of their home ranges from the previous season. Site fidelity within individual home ranges also varied;  $\geq 70\%$  of the core areas of some females were located in different sites within their home ranges during different seasons. Locations of females suggested a pattern of spatial avoidance among females during the wet season. Home-range overlap among males was extensive, both in the wet and dry seasons, suggesting that males did not maintain exclusive ranges. Overlap between males and females occurred both in the wet and dry seasons, and movements by females were not restricted within the ranges of individual males. Jaguars were located  $< 200$  m apart more often than expected, suggesting some degree of sociality. The reproductive profiles of females suggested either a low conception rate, a low survival rate of young, or that jaguars may be more social than previously thought. Interactions among males also suggested some degree of sociality.

Key words: activity patterns, home range, jaguar, movement rate, Pantanal, *Panthera onca*, social dynamics, spatial ecology

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Jaguars (*Panthera onca*) exist in distinct populations across a variety of habitats and regions (Sanderson et al. 2002). They are found in tropical and subtropical forests, semideciduous forests, thorny forests, scrublands, savanna, and swamps (Oliveira 1994; Sanderson et al. 2002). However, due primarily to land-use changes, habitat degradation, and habitat fragmentation, jaguars are now restricted to a fraction of their former range (Sanderson et al. 2002). Even now, remaining habitats are being converted to areas for agriculture and resource extraction. The Pantanal wetland of west-central Brazil is an important area for the conservation of jaguars and

a stronghold for the species (Sanderson et al. 2002; Soisalo and Cavalcanti 2006). In the Pantanal, traditionally large ranches have decreased in size while human access to jaguar habitat has increased as an infrastructure of roads has been built. This increasingly human-altered landscape will likely influence patterns of resource selection and space use by jaguars. Understanding their social dynamics and space use is important for conservation and management strategies to ensure their long-term survival and population persistence.

Previous studies provided insights into jaguar spacing, activity, and movements in the Pantanal (Crawshaw and Quigley 1991; Schaller and Crawshaw 1980). These authors noted that given the difficulties of their studies, their conclusions were speculative. Although our knowledge of jaguar ecology has increased since the 1st field studies in the mid-1980s, a detailed study of this cryptic species remains challenging. Most studies of jaguars have relied on small

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sample sizes or have been limited by logistics (Crawshaw and Quigley 1991; Schaller and Crawshaw 1980; Scognamiglio et al. 2002). Although locating animals from an aircraft improves coverage, high costs and weather conditions limit sampling strategies. Equally important is that aerial telemetry can only be done during the day, which may bias information about space use and movements of carnivores (Chavez and Gese 2006; Gese et al. 1990). Ground telemetry, although possible at night, is limited to accessible areas.

We studied the ecology of jaguars in the southern Pantanal using global positioning system radiocollars, which allowed us to simultaneously monitor several jaguars without direct observer intervention. We collected data on animal movements continuously, independent of weather, time of day, or season. In this paper, we examined space use, site stability and fidelity, movement rates, and interactions of jaguars, providing insights into their spatial and social ecology. Specific questions we addressed included: How large of an area does a jaguar use? How much spatial fidelity occurs seasonally among individual jaguars? What level of overlap exists between neighboring home ranges, and is space use exclusive? Is there spatial or temporal avoidance among jaguars? What is the frequency of social interactions between jaguars? Do social interactions between male and female jaguars indicate synchronous or asynchronous breeding?

## MATERIALS AND METHODS

*Study site.*—We conducted the study on a 460-km<sup>2</sup> cattle ranch in the southern Pantanal of Brazil, a vast 140,000-km<sup>2</sup> floodplain. Elevation ranges from 89 to 120 m above sea level. The climate is seasonal. The wet season occurs between October and March, with a mean monthly precipitation of 145 mm. The dry season occurs between April and September, with a mean monthly precipitation of 48 mm. The concentration of rains influences the level of the rivers, flooding large areas in the wet season. The hot and cool seasons coincide with the wet and dry seasons, respectively. Low temperatures reach 18.5°C in June–July and high temperatures reach 42.5°C in October. The vegetation is a mosaic, with influence from different vegetation biomes such as the cerrado in central Brazil, the Paraguayan Chaco, and the Amazon forest (Prance and Schaller 1982). Open fields are interspersed with isolated islands of secondary forest. Gallery forests border temporary and permanent rivers.

White-lipped peccaries (*Tayassu pecari*), an important prey species for jaguars, are abundant in the area, as well as caiman (*Caiman crocodilus yacare*), collared peccaries (*Pecari tajacu*), marsh deer (*Blastocerus dichotomus*), giant anteaters (*Myrmecophaga tridactyla*), and six-banded armadillos (*Euphractus sexcinctus*). During the dry season, cattle are widely dispersed throughout the study area. During the wet season, cattle are brought to drier areas, but still remain widespread. Cattle are unguarded and roam free during the day and night.

*Data collection.*—We captured animals with trained hounds at sites of frequent use as indicated by the presence of spoor during all seasons depending upon the water levels on the

study area. We immobilized treed jaguars using a dosage of 8 mg/kg of tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Animal Health, Fort Dodge, Iowa) combined with 2 mg/kg ketamine hydrochloride via a dart fired from a CO<sub>2</sub> pistol or a rifle. We examined each immobilized animal for general body condition, determined its sex and age, then measured, weighed, and fitted each jaguar with a global positioning system collar (Simplex; Televilt International, Lindsberg, Sweden), and released it at the site of capture. We estimated age based on the presence of milk or permanent dentition and tooth color and wear (Ashman et al. 1983). Procedures for animal capture and handling followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Between October 2001 and September 2002, we programmed the global positioning system collars to acquire a location every 2 h between 1800 and 0600 h (7 locations/day). Between September 2002 and April 2004, we programmed the collars to acquire 12 locations/day (every 2 h). We used a receiver (RX-900; Televilt International) to remotely download data from the collars every 3 weeks. Because of the extent of the study area and limited access on the ground, we used an aircraft for aerial location and data download. Occasionally, we located radio-collared jaguars from the ground with a 4-element, null-peak antenna system (White and Garrott 1990) mounted on a vehicle, or from horseback with a handheld antenna, to download data from the global positioning system collar. We recovered global positioning system collars for battery replacement using hounds as previously described. The global positioning system collars allowed for the simultaneous location of several individuals (within minutes of each other depending on satellite orbits) and provided an estimate of space use of each individual and documentation of social interactions.

We converted locations for individual jaguars from latitude and longitude into the Universal Transverse Mercator grid system using GeoCAD (GeoCAD Information, Ltd., Campo Grande, Brazil). We then plotted individual locations on a map of the study area (1:100,000) using ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). For comparisons with other studies, we estimated home-range sizes using the 98% minimum convex polygon method (Mohr 1947). However, these estimates were presented for the purpose of comparison only. For more accurate depictions of space use, we examined jaguar home ranges and their overlap using the 90% and 50% adaptive kernel estimator (Worton 1989) because this method has advantages over the minimum convex polygon method (Barg et al. 2005; Harris et al. 1990; Kenward et al. 2001; Seaman and Powell 1996). We considered a core area within the home range as the area enclosed by the 50% isopleth (Seaman and Powell 1996; Worton 1989). We used Home Range Extension (Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada) for ArcView 3.3 to estimate minimum convex polygon and kernel home ranges.

We estimated home-range size for each year because of differences in annual precipitation. Additionally, we calculat-

**TABLE 1.**—Seasonal space use (km<sup>2</sup>) of 10 jaguars (*Panthera onca*) as determined by the 50% and 90% adaptive kernel estimator, southern Pantanal, Brazil, 2001–2004 ( $n$  = number of locations). The 50% isopleth was considered the core area; the 90% isopleth was the home range.

Jaguar no.	Season and year														
	Wet 2001–2002			Dry 2002			Wet 2002–2003			Dry 2003			Wet 2003–2004		
	50%	90%	$n$	50%	90%	$n$	50%	90%	$n$	50%	90%	$n$	50%	90%	$n$
Female 1	9.1	43.0	576	24.4	88.7	963	14.8	99.4	486	—	—	—	—	—	—
Female 2	10.5	43.3	522	10.8	60.7	1,070	10.4	34.1	1,418	11.3	42.4	758	12.4	47.9	153
Female 3	—	—	—	—	—	—	—	—	—	—	—	—	28.1	100.8	512
Female 4	—	—	—	—	—	—	—	—	—	—	—	—	13.2	65.4	116
Male 1	46.2	192.0	265	53.0	252.8	752	—	—	—	—	—	—	—	—	—
Male 2	—	—	—	—	—	—	—	—	—	23.2	91.4	748	—	—	—
Male 3	—	—	—	—	—	—	—	—	—	36.2	163.8	453	—	—	—
Male 4	—	—	—	—	—	—	—	—	—	44.6	262.9	1,124	39.3	149.2	419
Male 5	—	—	—	—	—	—	—	—	—	—	—	—	20.8	79.0	645
Male 6	—	—	—	—	—	—	—	—	—	15.4	58.2	716	—	—	—

ed estimates of home-range size for each individual jaguar for each season throughout the study (i.e., wet season 2001–2002, dry season 2002, wet season 2002–2003, dry season 2003, and wet season 2003–2004). We defined the wet season as October–March and the dry season as April–September.

We compared overlap between individual home ranges and their core areas among the different seasons to examine home-range stability (90% isopleth) and fidelity of core areas (50% isopleth) to specific sites within a home range. We measured overlap among individual jaguars for each pair of individuals with overlapping home ranges and core areas for each season.

We used sequential locations collected every 2 h from collars on the 24-h relocation schedule to determine movement rates. The mean distance traveled per hour (km/h) was used in comparisons among individuals during different times of the day (dawn: 0400–0800 h; day: 1000–1400 h; dusk: 1600–2000 h; and night: 2200–0200 h) and during the different seasons using analysis of variance. Because of differences in annual precipitation levels, we analyzed the data for each year.

Home-range overlap is a large-scale approach of examining spatial avoidance, but does not account for temporal avoidance. We used locations collected simultaneously to determine if jaguars showed spatial or temporal avoidance of each other. We compared the mean distance between simultaneous locations (<1 min of each other) for each pair of jaguars with overlapping home ranges with the distance between them if the locations were randomly paired (Kitchen et al. 1999). For each pair of jaguars, we randomly paired all their locations (their expected distance if they were moving independently of each other) and compared that value to their simultaneous locations. We used a Student's  $t$ -test to compare the mean simultaneous distance between individuals with randomly paired locations (Kitchen et al. 1999). We assumed jaguars were avoiding each other if the simultaneous distances between them were significantly farther apart than the random locations. We performed this analysis for the different seasons during our study.

We also examined simultaneous locations of jaguars <200 m apart to identify the frequency of social interactions

between individuals, assuming they interacted when <200 m from each other (Kozłowski et al. 2008; Kramer and Bonenfant 1997; Louis and Le Berre 2000). We used the dates of male–female paired locations and the duration of such encounters to determine social interactions and estimate when possible mating events may have occurred.

## RESULTS

We captured 10 jaguars (5 adult males, 1 subadult male, and 4 adult females) and monitored them with global positioning system collars from October 2001 to April 2004 for 76 jaguar-months. Continuous monitoring periods for individual jaguars varied from 1.5 to 24 months. We monitored 3–5 jaguars at any time and obtained 11,787 locations on the 10 radiocollared individuals. We collected data during the wet seasons of 2001–2002, 2002–2003, and 2003–2004, and the dry seasons of 2002, 2003, and 2004; data from the dry season of 2004 were limited.

*Home-range size.*—The mean 98% minimum convex polygon home-range size for female jaguars during the wet seasons was  $57.1 \text{ km}^2 \pm 26.2 \text{ SD}$  ( $n = 7$ ; 95% confidence interval [95% CI]:  $30.9\text{--}83.3 \text{ km}^2$ ). Home-range size of females was  $69.1 \pm 28.7 \text{ km}^2$  ( $n = 3$ ; 95% CI:  $40.4\text{--}97.8 \text{ km}^2$ ) in the dry seasons. For male jaguars, the mean 98% minimum convex polygon home-range size was  $152.0 \pm 79.1 \text{ km}^2$  ( $n = 3$ ; 95% CI:  $72.9\text{--}231.1 \text{ km}^2$ ) during the wet seasons, and  $170.8 \pm 97.3 \text{ km}^2$  ( $n = 5$ ; 95% CI:  $73.4\text{--}268.1 \text{ km}^2$ ) during the dry seasons.

Estimates of 90% home-range size varied among study animals and seasons, ranging from 34.1 to 262.9 km<sup>2</sup> ( $\bar{X} = 104.2 \pm 71.3 \text{ km}^2$ ; Table 1). Among males, mean home-range size was  $140.0 \pm 57.0 \text{ km}^2$  (95% CI:  $83.0\text{--}197.1 \text{ km}^2$ ) in the wet seasons and  $165.8 \pm 92.3 \text{ km}^2$  (95% CI:  $73.5\text{--}258.1 \text{ km}^2$ ) in the dry seasons ( $t = 0.49$ ,  $d.f. = 6$ ,  $P = 0.32$ ). Home-range size of females averaged  $62.0 \pm 27.7 \text{ km}^2$  (95% CI:  $34.3\text{--}89.7 \text{ km}^2$ ) in the wet seasons and  $63.9 \pm 23.3 \text{ km}^2$  (95% CI:  $40.6\text{--}87.2 \text{ km}^2$ ) in the dry seasons ( $t = 0.11$ ,  $d.f. = 5$ ,  $P = 0.46$ ). There was no correlation between the 90% home-range

size and location sample size ( $r = 0.022$ ,  $F = 0.008$ ,  $d.f. = 1, 16$ ,  $P = 0.932$ ).

Within home ranges of females, core areas averaged  $14.5 \pm 6.5 \text{ km}^2$  (95% CI: 8.0–21.0  $\text{km}^2$ ; Table 1). The sizes of core areas for females during the dry ( $\bar{X} = 15.5 \text{ km}^2$ ) and wet seasons ( $\bar{X} = 14.1 \text{ km}^2$ ) were not different ( $t = -0.28$ ,  $d.f. = 3$ ,  $P = 0.40$ ). Among males, core areas averaged  $34.8 \pm 13.6 \text{ km}^2$  (95% CI: 21.3–48.4  $\text{km}^2$ ). For male jaguars, the size of the core area during the wet seasons ( $\bar{X} = 35.4 \text{ km}^2$ ) was not different from the size of the core area during the dry seasons ( $\bar{X} = 34.5 \text{ km}^2$ ;  $t = 0.09$ ,  $d.f. = 5$ ,  $P = 0.46$ ). There was no correlation between the 50% home-range size and location sample size ( $r = 0.052$ ,  $F = 0.044$ ,  $d.f. = 1, 16$ ,  $P = 0.837$ ).

The sizes of jaguar home ranges varied from year to year, both individually and among jaguars (Table 1). We examined individual home ranges among the different years of our study, because 2002 and 2003 were, respectively, the driest and the wettest of the last 8 years at the site. In the dry season of 2002, females 1 and 2 both increased their home ranges from the previous wet season (Table 1). However, during the following wet season of 2002–2003, female 2 reduced her home range, whereas female 1 increased hers. Although she increased her home range, female 1 decreased her core area. Female 2 followed that same pattern during the subsequent wet season (2003–2004), when she increased her previous dry season home range. However, in contrast to female 1, female 2 also increased her core area. Among all the females, female 3 had the largest home range within any season. She also was the female whose home range encompassed the driest portion of the site.

Both males for which we had consecutive wet and dry season home-range estimates (males 1 and 4) used smaller home ranges during the wet season (Table 1). In addition, the sizes of their core areas were consistent with the sizes of their home ranges. Males 1, 3, and 4, which had the largest home ranges among males, were also the oldest males among the radiocollared jaguars. Male 3, although much older than male 4, had a smaller home range in the dry season. Male 1 also was considerably older than male 4; however, the sizes of their home ranges were more comparable (Table 1). In contrast, subadult male 6, which had the smallest home range of any male in any season, was accompanied by his mother and sibling.

*Home-range stability and site fidelity.*—The stability of individual home ranges varied among seasons and individuals. Female 1 maintained 87% and 80% of her seasonal home ranges from the wet season 2001–2002 to the dry season 2002, and from the dry season 2002 to the wet season 2002–2003, respectively. In contrast, although female 2 maintained 93% of her home range in the following wet season (2002–2003), she used only 45% of the area from the previous season. She then maintained 90% of this new home range through the following dry season in 2003. In the wet season 2003–2004, she again used only 56% of the area she had used the previous dry season.

Within the home ranges they maintained from 1 season to another, the overlap of core areas also varied. Although female 1 maintained 80% of her home range from the dry season 2002 to the wet season 2002–2003, she maintained only 25% of the core area from the previous season; 75% of her core area was located in a different site. The same was true for female 2, which maintained most of her home range from the wet season 2001–2002 to the dry season 2002 but used only 22% of the core area the following season, meaning 78% of the core area was located in a different site within the home range. In the wet season of 2003–2004, her core area was located in a completely different area.

Among males, examination of our data also suggests that individuals behaved differently. Although male 1 maintained 99% of his home range between the wet season 2001–2002 and the subsequent dry season 2002, male 4 maintained only 37% of his home range between the dry season 2003 and the wet season 2003–2004. Although the overall area they used from 1 season to the next varied, males 1 and 4 maintained their core areas in similar proportions (43%). Unfortunately, our data set was limited to comparisons among individuals for which we had data for at least 2 consecutive seasons.

*Home-range overlap.*—Although radiocollared females used common areas throughout the period they were simultaneously monitored, the seasonal analysis of their locations suggested spatial avoidance between them. During the wet seasons 2001–2002 and 2002–2003, females 1 and 2 had distinct, nonoverlapping home ranges (Figs. 1A and 1B). Similarly, females 3 and 4, both monitored during the wet season of 2003–2004, did not overlap their home ranges with those of other radiocollared females. However, we documented overlap between home ranges of females during the dry seasons. During the dry season of 2002, females 1 and 2 overlapped their home ranges (Fig. 1C). The area overlapping both home ranges encompassed 23.3  $\text{km}^2$ , and represented one-fourth to one-third of the home ranges of females 1 and 2, respectively (Table 2). In addition to the 4 females we radiocollared, we indirectly monitored a 5th female (female 5), based on the locations of her young (subadult male 6). Therefore, assuming we can estimate her home range based on the locations of subadult male 6, his locations indicated that during the dry season of 2003, female 5 and her 2 offspring (subadult male 6 and a female sibling) overlapped with female 2 (Fig. 1D). The area of overlap encompassed 19.8  $\text{km}^2$  and represented 47% and 34% of the home ranges of females 1 and 5, respectively. Although we were unable to continuously monitor all radiocollared females throughout the study, or radiocollar every female in the study area, examination of our data suggests a pattern of spatial avoidance during the wet season.

Among male jaguars, extensive home-range overlap occurred both in the wet and dry seasons. The area of overlap between home ranges of any 2 male jaguars averaged  $78.1 \pm 20.2 \text{ km}^2$  (95% CI: 57.9–98.3  $\text{km}^2$ ). The most extensive overlap between home ranges of males occurred in the dry season 2003, between males 2 and 3, the oldest of the males

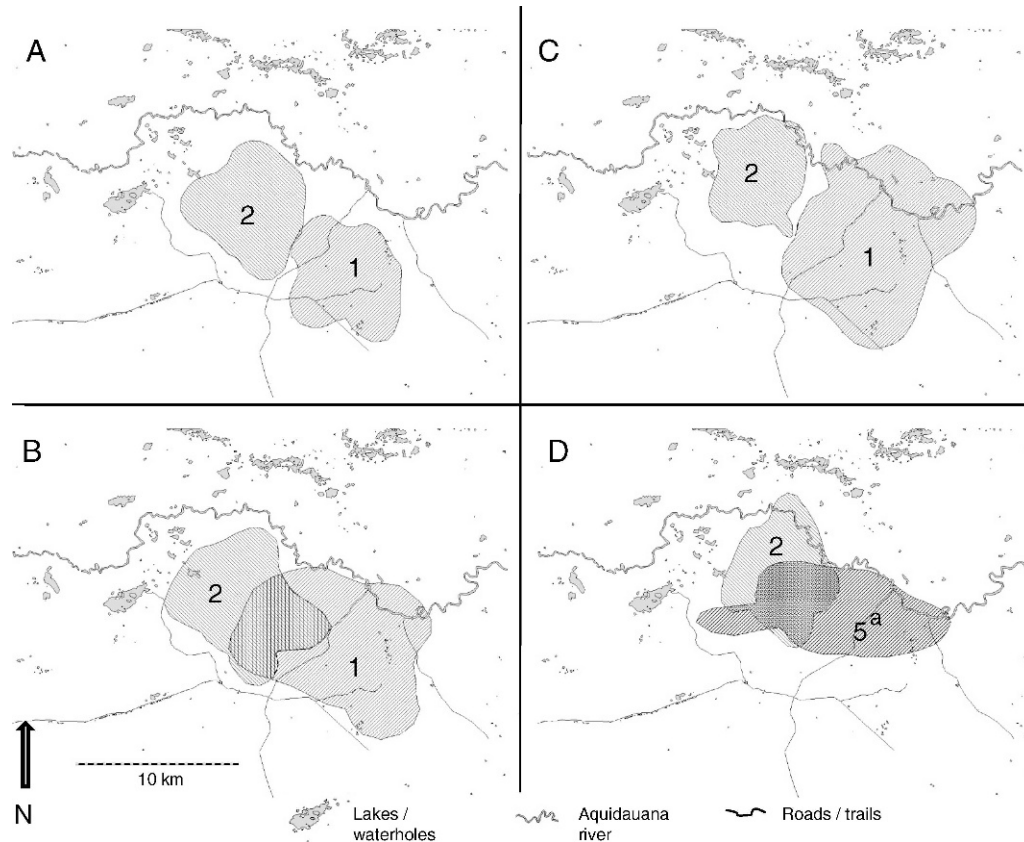


FIG. 1.—Seasonal home ranges (90% kernel isopleth) of female jaguars (*Panthera onca*) 1, 2, and 5, during A) wet season 2001–2002, B) dry season 2002, C) wet season 2002–2003, and D) dry season 2003, southern Pantanal, Brazil. <sup>a</sup> In addition to the 4 radiocollared females, we indirectly monitored a 5th female (female 5, panel D) via her young son (subadult male 6).

TABLE 2.—Area of overlap (km<sup>2</sup>) between the seasonal home ranges of jaguars (*Panthera onca*), southern Pantanal, Brazil. Data are presented for pairs of jaguars with overlapping home ranges during the wet seasons of 2001–2002, 2002–2003, and 2003–2004, and the dry seasons of 2002 and 2003. Columns 4 and 5 are percent overlap within their respective home ranges. F = female; M = male.

Jaguar pair (cat 1/cat 2)	Season and year	Area of overlap (km <sup>2</sup> )	% cat 1	% cat 2
F1/F2	Dry 2003	23.3	26	38
F1/M1	Wet 2001–2002	7.5	17	4
F2/M1	Wet 2001–2002	35.4	82	18
F1/M1	Dry 2002	41.2	16	46
F2/M1	Dry 2002	60.6	100	24
F2/M6	Dry 2003	19.8	47	34
F2/M2	Dry 2003	28.3	67	31
F2/M3	Dry 2003	42.4	100	26
F2/M4	Dry 2003	36.2	85	14
F2/M4	Wet 2003–2004	47.1	98	31
F4/M4	Wet 2003–2004	36.2	55	24
F2/M5	Wet 2003–2004	31.1	65	39
F4/M5	Wet 2003–2004	26.1	40	33
M2/M3	Dry 2003	68.9	75	42
M2/M4	Dry 2003	70.0	77	27
M2/M6	Dry 2003	43.5	48	75
M3/M4	Dry 2003	108.3	66	41
M4/M6	Dry 2003	45.6	17	78
M3/M6	Dry 2003	53.1	32	91
M4/M5	Wet 2003–2004	65.4	44	83

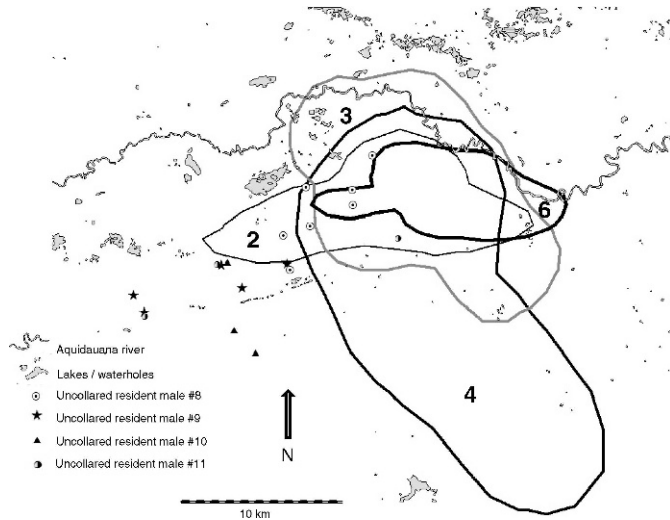


FIG. 2.—Home ranges (90% kernel isopleth) of radiocollared male jaguars (*Panthera onca*) 2, 3, 4, and 6 during the dry season of 2003, southern Pantanal, Brazil. Other symbols indicate locations of uncollared males photographed with camera traps.

monitored. However, all males in the dry season 2003 overlapped their home range with at least 3 other radiocollared individuals (Fig. 2), or at least 2 other radiocollared adult males, if we exclude subadult male 6, which was still accompanying his mother and sibling and may therefore not be considered an adult male with an established home range. The area of overlap shared by males 2, 3, and 4 was 65.4 km<sup>2</sup>, which represented 71%, 40%, and 25% of the home ranges of males 2, 3, and 4, respectively. In the wet season 2003–2004, the home ranges of males 4 and 5 overlapped by 65.4 km<sup>2</sup>, which represented more than one-half of their respective home ranges. Examination of our data suggests that younger individuals may have shared a larger proportion of their home ranges with same-sex conspecifics. In contrast with males 3

and 4, which overlapped 40% and 25%, respectively, males 2 and 5, the youngest of the adult males radiocollared, overlapped 71% and 83%, respectively, of their home ranges with other radiocollared males. Repeated photographs from camera trapping suggested the presence of an additional 4 resident males in the area (Fig. 2; Soisalo and Cavalcanti 2006).

Overlap between males and females occurred both in the wet and dry seasons. The area of overlap between the home ranges of a male and a female jaguar averaged 38.2 ± 13.0 km<sup>2</sup> (95% CI: 25.3–51.0 km<sup>2</sup>). On average, a male jaguar overlapped 27% of his home range with a female. In contrast, females overlapped an average of 64% of their home range with a male (Table 2). A larger portion of their home range was shared with opposite-sex conspecifics than same-sex conspecifics. In the dry season 2003, female 2 overlapped her home range with at least 3 adult males (males 2, 3, and 4) and her home range was entirely encompassed by the home range of male 3. During the wet season 2003–2004, she shared her home range with at least 2 adult males (males 4 and 5) and her home range was almost entirely encompassed by the home range of male 4 (Fig. 3). Female 4 also overlapped her home range with at least these same 2 males. She shared 55% and 40% of her home range with males 4 and 5, respectively.

*Activity patterns and movement rates.*—The mean rate a jaguar traveled per hour differed among time periods ( $F = 28.26$ ,  $d.f. = 3, 4,733$ ,  $P < 0.001$ ), with the highest rate of movement occurring at dusk ( $\bar{X} = 0.27$  km/h ± 0.5 SD). The mean rate of movement at dawn was 0.25 ± 0.6 km/h and at night was 0.23 ± 0.5 km/h. Although jaguar movement rates did not differ between dawn and night, they were different from movement rates during the daylight hours (Tukey's adjusted  $P < 0.001$ ), when jaguars traveled an average of 0.10 ± 0.4 km/h. Although the rate of movement by male and female jaguars did not differ during the day ( $t = 0.46$ ,  $d.f. = 567$ ,  $P = 0.64$ ), it was different during dawn ( $t = -3.10$ ,  $d.f.$

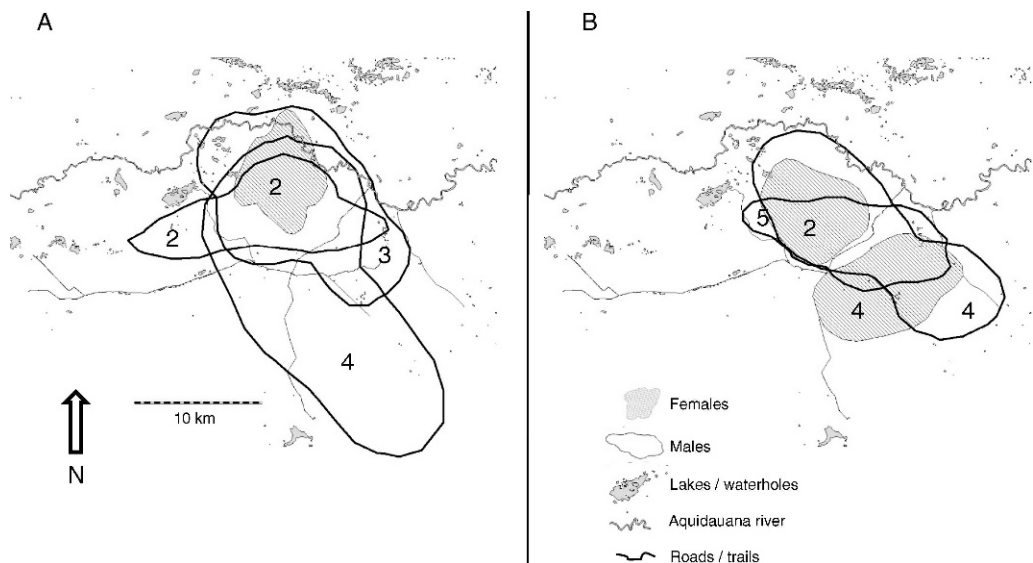


FIG. 3.—Home ranges (90% kernel isopleth) of A) female jaguar (*Panthera onca*) 2 and males 2, 3, and 4 during the dry season of 2003; and B) females 2 and 4, and males 4 and 5 during the wet season of 2003–2004, southern Pantanal, Brazil.

TABLE 3.—Distances (m) between jaguars (*Panthera onca*) with overlapping home ranges, southern Pantanal, Brazil, 2001–2004 ( $n$  = number of locations). F = female; M = male.

Jaguar pair	Season	Location pairing		$n$	$t$	$P$
		Simultaneous	Random			
F1/F2	Dry 2002	7,803	7,875	723	-0.451	0.65
F1/F2	Wet 2002–2003	8,860	9,078	374	-1.278	0.20
F1/M1	Wet 2001–2002	10,790	10,876	141	-0.219	0.83
F2/M1	Wet 2001–2002	7,525	7,271	122	0.562	0.57
F1/M1	Dry 2002	11,536	11,862	538	-1.146	0.25
F2/M1	Dry 2002	6,826	7,117	553	-1.197	0.23
F2/M6	Dry 2003	6,788	6,665	174	0.432	0.67
F2/M2	Dry 2003	6,725	6,666	306	0.243	0.81
F2/M3	Dry 2003	5,482	5,232	190	0.781	0.43
F2/M4	Dry 2003	10,920	10,865	348	0.118	0.91
F2/M4	Wet 2003–2004	9,013	8,865	38	0.133	0.89
F4/M4	Wet 2003–2004	6,566	7,087	24	-0.828	0.41
F2/M5	Wet 2003–2004	5,050	4,974	50	0.128	0.90
F4/M5	Wet 2003–2004	4,006	5,050	15	-1.353	0.19
M2/M3	Dry 2003	6,681	6,202	188	1.236	0.22
M2/M4	Dry 2003	8,477	8,666	429	-0.427	0.67
M2/M6	Dry 2003	4,923	4,464	278	1.621	0.11
M3/M4	Dry 2003	10,790	11,143	212	-0.575	0.57
M4/M6	Dry 2003	5,534	5,335	435	1.084	0.28
M3/M6	Dry 2003	5,760	6,008	87	-0.868	0.39
M4/M5	Wet 2003–2004	7,134	7,246	120	-0.254	0.80

= 1,177,  $P = 0.002$ ), dusk ( $t = -3.67$ ,  $d.f. = 1,357$ ,  $P < 0.001$ ), and night ( $t = -7.61$ ,  $d.f. = 1,628$ ,  $P < 0.001$ ), with males moving at a higher rate than females. There was no difference in jaguar movement rates across the seasons during dawn ( $F = 1.35$ ,  $d.f. = 4, 1,174$ ,  $P = 0.25$ ), day ( $F = 2.49$ ,  $d.f. = 3, 565$ ,  $P = 0.06$ ), or dusk ( $F = 1.91$ ,  $d.f. = 4, 1,354$ ,  $P = 0.11$ ). However, their movement rates differed among seasons during the night ( $F = 2.89$ ,  $d.f. = 4, 1,625$ ,  $P = 0.02$ ), with the highest rate occurring in the wet season of 2001–2002 ( $\bar{X} = 0.27$  km/h), followed by the wet season of 2003–2004 ( $\bar{X} = 0.25$  km/h).

*Spatial and temporal associations.*—We investigated spatial and temporal avoidance between jaguars by comparing the mean distance between simultaneous locations of individual jaguars with the mean distance between them if randomly paired (Kitchen et al. 1999). We calculated distances for 2 pairs of jaguars in the wet season 2001–2002, 3 pairs in the dry season 2002, 1 pair in the wet season 2002–2003, 10 pairs in the dry season 2003, and 5 pairs in the wet season 2003–2004. Distances between simultaneous locations of 2 jaguars did not differ from those if randomly arranged in any season (Table 3), suggesting they moved independent of each other, neither avoiding nor attracting each other.

*Social interactions.*—We assumed that jaguars located <200 m from each other may have had a social encounter. Among the paired locations <200 m apart, there were 32 possible interactions between a female and a male jaguar, 21 pairs of locations between 2 males, and only 1 possible encounter between 2 females. However, 1 of the males involved was subadult male 6, which was accompanied by his mother and female sibling; these interactions could have been between the entire family and another male.

*Interactions between males and females.*—We used the dates of male–female encounters and the duration of such interactions, as well as the reproductive status of the female during capture to estimate when possible mating events may have occurred. In addition, we used clusters of female locations at a particular site as evidence of possible dens and the estimated age of young captured with their mothers to create a reproductive profile of radiocollared female jaguars.

When captured for the 1st time in November 2000, female 1 was accompanied by an adult male (male 7, also captured on the same day as female 1, but equipped with a traditional very-high-frequency radiocollar and therefore not included in this paper) and exhibited several scratch marks behind her neck and on her shoulders, characteristic of mating behavior (S. M. Cavalcanti, pers. obs.). Between September and October 2001, she was repeatedly located in a restricted area of approximately 160 m<sup>2</sup> for about 7 weeks, suggesting she had given birth to a litter. During her recapture at the end of October 2001, she was accompanied by a 2-month-old female cub. Given the approximate gestation period of 90–111 days (Ewer 1973; Hemmer 1979), this female had therefore mated around May–June 2001. Either she did not get pregnant from the November 2000 encounter with male 7, or she lost the litter. This female was subsequently located in the company of male 1 on 2 different occasions, for at least 4 h in April 2002 and for 3 consecutive days during May 2002. The distances between their simultaneous locations ( $\bar{X} = 3.4$  m  $\pm$  4.0 SD) and the length of their association suggested they could have been mating. If she had lost her 2001 litter, she could have gotten pregnant again and a 3rd litter could have been born in August–September 2002. However, she associated with yet another male around February–March 2003, as she was



pregnant during her recapture in April. We unfortunately lost contact with her radiocollar in May 2003.

Female 2 was in the company of an adult male when she was captured in December 2000, as indicated by fresh pugmarks. During her recapture in October 2001, she was pregnant suggesting she had mated in September. Her litter would have been born around January 2002. In September 2002, we recaptured this female in the company of a 7-month-old male cub. However, 1 and 3 weeks before her recapture, this female was located with male 1 for periods of 6 h and 2 h, respectively. She associated again with this same male for 3 days (2 days after her recapture). The distances between their simultaneous locations averaged  $30 \pm 24$  m. In June 2003 she had encounters with 2 different adult males, males 3 and 4, for 16 h and 4 h, respectively. In the beginning of July 2003, this female was located in a restricted area for 12 consecutive days, suggesting she may have had another litter. Because gestation is 90–111 days, her mating event could have been near the end of March or the beginning of April 2003. Therefore, she was probably already pregnant when she associated with males 3 and 4 in June. From 30 November to 8 December, she was again located in the company of male 4 on 2 different occasions. When she was recaptured on November 20, she was in heat and had recently (<1 day) been mating. Four months later in March 2004, female 2 was once more located in the company of an adult male (male 5) for 6 consecutive hours.

Female 4 was accompanied by male 5 the day she was 1st captured in November 2003. She was again located with him a month after her capture, although for only a 2-h period. Five months later (May 2004), she spent 5 days in the company of male 4. Although by this time both female 4 and male 5 were wearing traditional very-high-frequency radiocollars, and we therefore could not get accurate distances between their locations. Despite not being able to establish visual contact with them, their vocalizations (meowing characteristic of domestic cats in estrus) suggested they could have been mating during this period.

On another occasion, male 1 was located in a cluster of locations that we later determined to be an interaction with a noncollared female. We obtained a photograph of male 1 accompanied by a noncollared female that was acquired at the same location with date and time coinciding with the male's locations.

Additional information from camera traps suggested that females can come in contact with adult males before their young disperse. We photographed subadult male 6 accompanied by its mother and female sibling days after photographing her walking together with an adult male (male 4—Soisalo and Cavalcanti 2006). In addition, locations of male 6 were associated with signs of a family group, such as large day beds.

*Interactions between male jaguars.*—On 1 occasion, we were able to detect 2 adult male jaguars (males 2 and 3) sharing the carcass of a feral hog. It was difficult to detect which one was responsible for the kill because their locations

overlapped with regard to date and time. Given their difference in age ( $\geq 4$ –5 years apart), we assumed these 2 males were not brothers from the same litter. On 3 other occasions, males 2 and 4 were located 24, 150, and 198 m from each other. We were unable to find any carcasses of prey in the vicinity of their locations. In August 2003, these same 2 males were located 30 m from each other for a period of 40 h. Again we did not find any carcasses of prey in the area.

We found male 3 dead after monitoring him for 3 months. From the constant vocalizations by at least 3 different individuals we heard the night before his death, in addition to hemorrhage and puncture marks on his skull and other parts of the body, we concluded he died as a result of an aggressive encounter with another male(s).

## DISCUSSION

Activity patterns and movements of jaguars have been previously documented (e.g., Crawshaw and Quigley 1991; Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980). Generally, jaguars are characterized as nocturnal (Almeida 1976; Mondolfi et al. 1986; Nowak and Paradiso 1983), although Crawshaw and Quigley (1991) reported jaguars to be more diurnal. However, they included dawn and dusk movements as part of daytime activity, whereas other researchers considered these as nighttime activity. Nevertheless, these authors reported distinct activity peaks at dawn, noon, and dusk. In contrast, we found that jaguars were active at dawn and dusk, and traveled less during the day. In the study by Crawshaw and Quigley (1991), although there were no differences in activity between seasons, jaguars appeared to be more active during the day in the wet season. In our study, there was no difference in their movement rates at dawn, dusk, or day across the seasons. During the wet season, the jaguars moved at a higher rate at night.

Despite increased knowledge of jaguar ecology since the 1st studies in the 1980s, information about their spatial dynamics remains scarce. In addition to birth and death rates, and immigration and emigration, the density of a jaguar population in an area also depends on the type of land-tenure system, especially the sizes of their home ranges and the degree to which they overlap. These factors, in turn, are influenced by different ecological conditions. Some authors have suggested that the distribution and abundance of prey are the major ecological factors influencing the social organization of carnivores (Sunquist and Sunquist 1989).

Previous studies have shown wide variation in home-range sizes of jaguars (e.g., Crawshaw et al. 2004; Crawshaw and Quigley 1984; Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980). According to Hoogsteijn and Mondolfi (1992) these large differences in jaguar home-range sizes reflect the abundance of prey in a given habitat and the necessary movements by a jaguar to find prey. However, other factors play important roles in the spatial structure of a population. Sandell (1989) suggested that territories of females are determined by food abundance and distribution,

whereas territories of males are determined by the distribution of females. In their study in the Pantanal, Crawshaw and Quigley (1991) suggested that the smaller home ranges of jaguars during the wet season reflected the concentration of their food resources to islands of dry land. The foraging ecology of jaguars in the area suggested that the most important native prey species for jaguars (i.e., caiman and peccaries) were more widespread during the wet season (Coutinho and Campos 1996; Fragoso 1998). Cattle also were a significant prey item for jaguars and during the wet season they were confined to islands of dry ground; however, predation rates by jaguars were higher during the dry season when cattle were more widespread. Another factor that could cause female jaguars to reduce their home ranges during the wet season is the need for dry ground on which to raise their young and the limited mobility of a litter. The Pantanal usually receives >800 mm of rainfall during the wet season, inundating much of the floodplain for several months and limiting the availability of dry ground on the landscape.

For both males and females, the size of the core areas during the wet season was not different from those during the dry season. However, site fidelity within the home range varied considerably. Although female jaguars maintained their overall home ranges, they often changed the areas they used most intensively. There may be <1 preferred denning or resting site within the home range of a female and therefore site fidelity may not be strong.

Studies on the social ecology of solitary cats such as tigers (*Panthera tigris*), leopards (*Panthera pardus*), and mountain lions (*Puma concolor*) suggest that the basic pattern of social organization in felids is one in which males occupy large, exclusive or little-overlapping ranges encompassing the home ranges of several females (Bailey 1993; Seidensticker et al. 1973; Sunquist 1981; Sunquist and Sunquist 1989). Our results suggest that male jaguars did not retain exclusive ranges but overlapped extensively year-round. Previous studies on jaguars in the Pantanal (Crawshaw and Quigley 1991; Schaller and Crawshaw 1980) either had sample sizes too small to observe overlap among males, or based their conclusions on the locations of pugmarks and other indirect signs. Rabinowitz and Nottingham (1986) documented overlap among home ranges of males in Belize and suggested that male jaguars had a dynamic land-tenure system that constantly changed whenever established ranges became vacant. Nevertheless, all solitary felids encounter a variety of habitat types varying in resource distribution and availability. As a result, their land-tenure systems may exhibit some level of flexibility.

Sandell (1989) suggested that solitary males may have overlapping ranges if density of females is low. Results from camera-trap surveys in our study area conducted in 2003 and 2004 (Soisalo and Cavalcanti 2006) suggested that male:female ratios during those years were 1.5:1 and 1.2:1, respectively. In solitary carnivore species, roaming over large areas by males may increase their reproductive success because they increase the number of females with which they can mate (Davies 1978; Lott 1984). Ostfeld (1985) argued that

the spacing strategies of males depends solely on the spatial distribution of reproductive females and predicted that males would have overlapping home ranges when female distribution was not clumped (i.e., evenly distributed). Ims (1987) argued that in addition to the spatial component, female distribution also has a temporal component, suggesting that the number of reproductive females may vary both in time and space. Therefore, when female receptivity is asynchronous, males may have large, overlapping home ranges. In addition, mating with different males could be a strategy adopted by females to increase paternal uncertainty, thereby reducing the loss of their young to infanticidal males (Ebensperger 1998).

Examination of our data suggested that females have nonoverlapping home ranges during the wet season. Additionally, their reproductive profile indicated a lack of an established mating season (i.e., females were found pregnant in April and October; cubs were documented born in September, January, and July), allowing them to associate with males throughout the year. We found on average, that a female overlapped 64% of her home range with the home range of a male, suggesting that their home ranges, and therefore their movements, were not restricted within the ranges of individual adult males as previously suggested (Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980). Therefore, we suggest that the mating system in jaguars may be of a polygynous and promiscuous nature; the frequency of social interactions we documented suggested that males associated and possibly mated with several females, whereas females associated and possibly mated with several males.

The frequency with which females associated with males suggests either a low survival rate of young, or that jaguars may be more social than previously thought. As Leyhausen (1965) describes, "solitary" is not necessarily the opposite of "social." A species may be considered solitary, but an individual may eventually meet with conspecifics. Schaller and Crawshaw (1980) described 4 jaguars hunting for a week in the same small area. They also described sightings of a male with a female and 2 large cubs and several sightings of 2 males, indicating a social life beyond courtship and the raising of a litter. The associations between the radiocollared animals in the present study, male 1 and female 2, during a period in which she was accompanied by her 6- to 7-month-old cub, corroborates this possibility. Male-male associations away from carcass sites also may suggest some degree of sociality, although these instances could be related to courtship behavior involving a noncollared female.

Studies to date, hindered by logistics and difficulties inherent to studying large carnivores, could have provided an incomplete picture of the social organization of jaguars. Analyses of total home ranges fail to identify intricacies of territorial behavior. Examination of our data provided insight into the dynamic nature of the land-tenure system of jaguars and their social interactions. Nevertheless, future research would benefit from radiocollaring more individuals and monitoring them for a longer time to determine long-term

jaguar space use. Only then will we be able to fully understand their spatial ecology and social dynamics. Understanding how different ecological variables influence the land-tenure system of jaguars will be important for the long-term conservation of this secretive carnivore.

## RESUMO

O Pantanal é uma área importante para a conservação da onça-pintada (*Panthera onca*). Com a diminuição no tamanho das grandes fazendas tradicionais, o acesso à áreas de uso da onça-pintada aumenta, resultando em paisagens alteradas que podem influenciar os padrões de seleção de recursos pela onça-pintada, assim como o seu uso do espaço. Para estudar a onça-pintada no sul do Pantanal, utilizamos rádiocolares equipados com sistema de posicionamento global. Capturamos e equipamos com rádio 10 onças-pintadas (6 machos e 4 fêmeas), obtivemos 11.787 localizações, e examinamos o uso do espaço, taxas de movimentação, e interações sociais entre os indivíduos, entre outubro 2001 e abril 2004. Estimativas das áreas de vida (90% kernel) variaram entre indivíduos e estações do ano (variação: 34,1 a 262,9 km<sup>2</sup>). Os tamanhos das áreas-núcleo (50% das localizações) de ambos machos e fêmeas não mostraram diferenças entre as estações, mas as áreas de vida (90% das localizações) durante as secas foram geralmente maiores do que durante as cheias. A estabilidade das áreas de vida variaram tanto entre época do ano quanto entre indivíduos. Algumas fêmeas mantiveram  $\geq 80\%$  de suas áreas de vida de uma estação para a outra, enquanto outras usaram  $\leq 50\%$  de suas áreas de vida da estação prévia. A fidelidade para com áreas específicas dentro da área de vida também variou;  $\geq 70\%$  das áreas-núcleo de algumas fêmeas se localizaram em diferentes porções da área de vida em diferentes estações do ano. A análise das localizações das fêmeas sugeriram um padrão de exclusividade em suas áreas de vida durante as cheias. A sobreposição das áreas de vida dos machos se mostrou bastante extensa, tanto nas secas quanto nas cheias, sugerindo que os machos não mantêm áreas de vida exclusivas. Sobreposições entre machos e fêmeas ocorreram tanto nas secas quanto nas cheias, e os movimentos das fêmeas não se restringiram às áreas de vidas de nenhum macho em particular. As onças-pintadas foram localizadas  $< 200$  m entre si com uma frequência maior do que a esperada, sugerindo um certo grau de sociabilidade. O perfil reprodutivo das fêmeas sugeriu ou uma baixa taxa de concepção, ou uma baixa taxa de sobrevivência dos filhotes, ou ainda que as onças-pintadas possam exibir um comportamento mais sociável do que previamente se acreditava. Interações entre machos também sugeriram um certo grau de sociabilidade.

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