

Comparative Ecology of Jaguars in Brazil

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To understand the ecology of the jaguar in Brazil, we compared its diet, home range, abundance, activity patterns and habitat use among biomes, using the existing literature. Jaguars preferably feed on medium to large sized prey, but can adapt to the existing fauna in the different biomes. Mean home ranges vary from 49.4 km² (females, Pantanal) to 265 km² (males, Cerrado). Density values range from 2.00 individuals/100km² in the Cerrado to 6.7 individuals/100km² in the Pantanal. In general, jaguars show a preferably crepuscular-nocturnal activity, but can also be active during the day. Across the different biomes, the species uses more closed vegetation associated with water and avoids agriculture and pasture lands. While there is still a lack of studies in the Amazon, Cerrado and the Caatinga, the results provide insight into the species' adaptability, as well as baseline information for landscape scale jaguar conservation efforts.

Contributing almost 50% to the jaguar's current distribution, Brazil presents the largest variety of habitats with jaguar occurrence. Of the country's six biomes, the species can still be found in five: The Amazon rainforest, the semi-arid Caatinga, the Cerrado grasslands, the Pantanal floodplain, and the coastal Atlantic Forest. With their differences in habitat and prey base, jaguar ecology should differ widely among these biomes. Since the first studies of jaguars in the wild in the Brazilian Pantanal (Schaller & Vasconcelos 1977, Schaller & Crawshaw 1980), there has been a considerable increase in the amount of research in different aspects of jaguar ecology. With the intention of revealing ecological differences, we used the existing literature to compare jaguar diet, home range, density, habitat use, and activity pattern between biomes.

Diet

The jaguar is considered opportunistic in its feeding habits (Seymour 1989), with more than 85 prey species described so far (Sunquist & Sunquist 2002). Throughout its range, the species primarily feeds on medium to large prey species (López González & Miller 2002). Table 1 shows the results from 15 different jaguar diet studies from Brazil.

In the Atlantic Forest, white-collared peccaries (Guix 1997, Leite & Galvão 2002, Azevedo 2008), deer (Leite & Galvão 2002, Azevedo 2008), armadillos (Facure & Giaretta 1996) and white-lipped peccaries (Guix 1997, Garla *et al.* 2001) were the most frequently

consumed species. With the exception of one study (Facure & Giaretta 1996) showing an important presence of the giant anteater, this and other large species such as tapirs and capybaras are almost absent in the jaguar's diet in this biome. With its highly fragmented landscape under strong human pressure, cattle can become the single most important prey in terms of frequency of occurrence (almost 40%, Guix 1997) or biomass consumed (26%, Azevedo 2008).

Likewise, in the Pantanal, where jaguars coexist with domestic cattle, this can become an important part of the jaguar's diet (Almeida 1984, Crawshaw & Quigley 2002, Dalponte 2002), constituting up to 48% of the consumed items (Crawshaw & Quigley 2002). Jaguars in the Pantanal also prey abundantly on wild species. In general, the capybara

(Fig. 1) seems to be the most frequently consumed large prey species (Dalponte 2002, Azevedo & Murray 2007), followed by deer (Dalponte 2002, Azevedo & Murray 2002) and white-lipped peccary (Crawshaw & Quigley 2002), while coati is the most frequently consumed medium prey (Dalponte 2002). Although probably more abundant than any of the mammalian prey species, caimans (*Caiman yacare*) are not consumed more frequently (e.g. Azevedo & Murray 2007).

In the Amazon, studies in two distinct areas show considerable differences in jaguar diet, probably due the distribution and abundance of prey species. In the seasonally flooded Várzea marshlands, jaguar prey consists of a small number of arboreal species, like sloths, and species associated with water, like caimans



Fig. 1. Capybaras represent an important prey species for jaguars in the Pantanal (Photo L. Leuzinger, Fazenda Barranco Alto).

Caiman crocodilus and *Melanosuchus niger*, and their eggs (Ramalho 2006). On the other hand, in areas with influence from the neighboring Cerrado biome, jaguars prey on a large number of species, with tapirs, peccaries and cattle making up the largest part of consumed biomass (Nuno 2007).

Large prey species seem to become even more important in the Cerrado, where jaguar diet consisted exclusively of the six larger prey species found locally; white-lipped peccaries and giant anteaters constitute 49% to the consumed biomass (Silveira 2004). While the open Cerrado habitat favors the abundance of these large grassland species, their complete dominance of the jaguar's diet may be peculiar to the study site, a protected area surrounded by large-scale crop plantations, which knowingly serve as an abundant food source for local herbivores.

Finally, the only study case in the Caatinga, a vast xeric biome characterized by frequent periods of long, severe droughts, found that jaguars are opportunistically preying on available large-

sized species such as giant anteaters, as well as smaller prey like the abundant armadillos (Olmos 1993).

Judging from frequency of occurrence in scats and from mean prey weight (Table 1), in both the Amazon and Atlantic Forest, smaller prey species seem to be more important than in the Pantanal and Cerrado biomes, characterized by open habitat. The frequency of medium and small prey items in the Caatinga demonstrates adaptation to an environment where large mammals are scarce. The variation in frequency of certain prey species within biomes reflects differences in diet on a smaller scale, again indicating the jaguar's opportunistic feeding behavior – in the Amazon, the species has even been reported to prey on freshwater dolphin (*Inia geoffrey*; Silveira *et al.* 2004).

Home Range

Home ranges and spacing patterns of solitary carnivores are influenced by the availability, distribution and seasonality of favorable habitat, food, and reproductive resources, as well as inter and in-

traspecific interactions (Sandell 1989). Jaguar home range size and spacing has been studied in the Pantanal, Cerrado and Atlantic Forest, and Table 2 shows the result of the different home range size and overlap estimates among these studies.

Due to the large variation of home range size within biomes and even within study sites, combined with the different estimators used, it is hard to affirm that differences are ecologically based rather than methodological artifacts. However, there is a demonstrated tendency for home ranges in the Pantanal to be smaller than those in the Atlantic Forest or Cerrado.

While open habitat is generally associated with larger home ranges (reviewed by Silveira 2004), the comparatively smaller home ranges observed in the Pantanal may correspond mostly to a more abundant and uniformly distributed prey base (Azevedo & Murray 2007), as the Pantanal is known for its rich and abundant fauna (Swartz 2000). The observed degree of intrasexual overlap of approximately 50% indicates

Table 1. Frequency of occurrence (%) of prey species in jaguar scats from different diet studies in Brazil; value represents mean frequency for the particular species of all studies in the respective biomes, values in brackets give minimum and maximum reported values; mean prey weight (MPV) is the mean from all studies providing this value. (N.A. = Not available)

BIOME	Atlantic Forest	Pantanal	Amazon	Cerrado	Caatinga
References	(1-6)	(7-11)	(12,13)	(14)	(15)
<i>Small prey (< 2kg)</i>					
Mammals	2.5 (3.9 – 11.3)	0.4 (0.0 -1.9)	7.8 (0.0 – 15.6)	0.0	0.0
Reptiles	1.3 (1.4 – 6.6)	0.0	6.9 (6.3 – 7.5)	0.0	0.0
Others	5.6 (1.4 – 14.3)	2.8 (0.0 – 7.2)	3.0 (0.0 – 6.0)	0.0	14.3
<i>Medium prey (2-10 kg)</i>					
Monkeys (general)	0.4 (0.9 – 1.4)	0.0	11.3 (10.0 – 12.5)	0.0	0.0
Coati (<i>Nasua nasua</i>)	7.2 (5.7 – 27.4)	8.6 (4.8 – 38.4)	0.0	0.0	0.0
Crab-eating raccoon (<i>Procyon cancrivorus</i>)	1.8 (2.0 – 8.6)	0.8 (0.0 – 4.8)	1.6 (0.0 – 3.1)	0.0	0.0
Armadillos (<i>Dasyus</i> sp and others)	9.1 (8.5 – 22.0)	0.0	1.6 (0.0 – 3.1)	0.0	14.3
Sloth (<i>Bradypus variegatus</i>)	0.4 (0.0 – 2.1)	0.0	20.5 (0.0 – 41.0)	0.0	0.0
Others	11.6 (0.0 – 33.4)	4.6 (0.0 – 8.0)	12.5 (0.0 – 25.0)	4.0	0.0
<i>Large prey (>10 kg)</i>					
Tapir (<i>Tapirus terrestris</i>)	2.2 (0.0 – 12.5)	0.4 (0.0 – 2.0)	3.2 (0.0 – 6.3)	4.0	0.0
Capybara (<i>Hydrochaeris hydrochaeris</i>)	1.6 (1.4 – 7.9)	47.5 (14.0 – 100.0)	0.0	0.0	0.0
White-lipped peccary (<i>Tayassu pecari</i>)	7.6 (0.0 – 17.9)	7.2 (0.0 – 22.0)	3.1 (0.0 – 6.3)	35.0	0.0
White-collared peccary (<i>Tayassu tajacu</i>)	23.2 (7.8 – 37.5)	2.9 (0.0 – 9.0)	3.1 (0.0 – 6.3)	0.0	14.3
Giant anteater (<i>Myrmecophaga tridactyla</i>)	9.5 (0.0 – 57.1)	0.9 (0.0 – 2.4)	1.6 (0.0 – 3.1)	30.0	57.1
Rhea (<i>Rhea americana</i>)	0.0	0.2 (0.0 – 0.8)	0.0	13.0	0.0
Deers (<i>Mazama</i> sp. and others)	8.8 (2.8 – 23.7)	8.3 (0.0 – 26.4)	0.0	13.0	0.0
Caiman (general)	0.0	7.2 (0.0 – 23.0)	22.8 (3.1 – 42.5)	0.0	0.0
Livestock	13.8 (0.0 -37.5)	20.2 (0.0 – 48.0)	4.4 (2.5 – 6.3)	0.0	0.0
Others	0.0	0.8 (0.0 - 4.0)	8.5 (0.0 -17.0)	0.0	0.0
MWP (kg)	11.8	14.0	5.4	84.7	N.A.

References: 1) Crawshaw 1995; 2) Facure & Giaretta 1996; 3) Guix 1997; 4) Garla *et al.* 2001; 5) Leite & Galvão 2002; 6) Azevedo 2008; 7) Crawshaw & Quigley 2002; (8, 9 and 10) Dalponte 2002; 11) Azevedo & Murray 2007; 12) Ramalho 2006; 13) Nuno 2007; 14) Silveira 2004; 15) Olmos 1993.

Table 2. Jaguar home range size (min - max) and overlap (F = overlap between females, M = overlap between males) estimates from the Pantanal, Cerrado, and Atlantic Forest, and means calculated for each biome, with sample (N).

Habitat	Home Range (km ²)	Mean Home Range (km ²)		Degree of overlap	Reference
		Males (N)	Females (N)		
Pantanal (A)	25 – 90	90 (1)	32.3 (3)		Schaller & Crawshaw 1980
Pantanal (A)	97.1 – 168.4	152.4 (1)	139.6 (4)	42% F	Crawshaw & Quigley 1991
Pantanal (B)	52 – 176	116.5 (4)	58.5 (2)		Soisalo & Cavalcanti 2006
Pantanal (D)		67.4 (3)	32.2 (5)	49.7% M, 52.9% F	Azevedo & Murray 2007
Pantanal (B)	1.41 – 122.2	79.6 (3)	49.4 (8)	44% F	JCF (unpub. data)
Mean Pantanal		101.2	62.4	49.7% M, 46.3% F	
Cerrado (C)	228 – 265	265 (2)	228 (1)	81.8% M ^A	Silveira 2004
Atlantic Forest (A)	8.8 – 138	88.7 (4)	39.4 (2)		Crawshaw 1995
Atlantic Forest (A)	43.8 – 177.7	102 (2)	87.3 (5)	6% M, 18% F	Cullen <i>et al.</i> 2005
Atlantic Forest (E)*	87 – 173	147 (1)	130 (2)	15% F	Cullen 2006*
Mean AF		112.6	85.6	6% M, 16.5% F	

A) Minimum Convex Polygon (MCP) at 100% of locations; B) Minimum Convex Polygon (MCP) at 95% of locations; C) Minimum Convex Polygon (MCP) at 80% of locations; D) Fixed Kernel at 95% of locations; E) Fixed Kernel at 85% of locations. * To avoid autocorrelation with the study presented in Cullen *et al.* 2005, we used only data from another area which was not included in the previous work.

the presence of regions of exclusivity in jaguars' home ranges (Azevedo & Murray 2007), which is expected in solitary carnivores when food resources are abundant and uniformly distributed and the cost of defense of such a core area is lower than the benefit of an exclusive use of the resource present in it (Sandell 1989).

Home range estimates for the Cerrado are on average 2.6 (males) to 3.6 (females) times larger than in the Pantanal (Table 2). While several large prey species are common in the Cerrado study site at Emas National Park (ENP), their abundance is considerably lower than in the Pantanal (Silveira 2004). Also, the habitats preferentially used by jaguars are restricted, and in ENP males have been observed to occasionally travel more than 40 km from regular home ranges, probably to find mates (Silveira 2004). Several individual jaguars made use of the same preferred habitat patches, a pattern expected when resources are aggregated (Sandell 1989). This could explain the high degree of range overlap observed (Table 2). Emas National Park, as most areas of suitable jaguar habitat in the Cerrado, is largely isolated by farmland, forcing resident jaguars to live under an ecological stress (Soares *et al.* 2006) that could be affecting their spacing patterns (Silveira 2004).

In the Atlantic Forest - the most degraded and fragmented biome of Brazil - jaguar spacing patterns seem to be influenced by human activities (Craw-

shaw 1995; Cullen 2006). Jaguars generally establish core areas of their home ranges within the limits of protected areas or in remaining patches of native habitat. The larger home ranges come from a study site influenced by the nearby Cerrado, whose semi-deciduous, dry vegetation is characterized by a low carrying capacity for herbivores and consequently for carnivores. Home range estimates from areas with more typical Atlantic Forest vegetation are unambiguously smaller (Crawshaw 1995).

Throughout Brazil, female jaguars' home ranges are consistently smaller than males', reflecting the species' polygamous breeding system. While home range size for a female is determined by her and her offspring's metabolic demands, male ranges are determined by the distribution of females (Fig. 2).

Males generally overlap ranges of various females (Sandell 1989).

Abundance

Abundance of large terrestrial mammals like the jaguar seems to be regulated most often by their food supply (Sinclair 1989). Because abundance has to refer to area to be comparable among studies, density is often used as a surrogate value. Table 3 shows jaguar density estimates for the different Brazilian biomes, based on radio-telemetry and camera trapping studies. Whenever more than one estimate per study was given, we used the value considered the best by the authors.

Consistent with smaller home ranges, the highest jaguar densities are supported in the Pantanal (Schaller & Crawshaw 1980, Crawshaw & Quig-

Table 3. Jaguar density (ind./100 km²) estimates based on radio-telemetry data and camera-trapping in different biomes of Brazil.

Biome	Methodology	Density ± SE	Reference
Atlantic Forest	Telemetry	3.70	Crawshaw 1995
Atlantic Forest	Telemetry	2.33	Cullen <i>et al.</i> 2005
Atlantic Forest	Camera-traps	2.22 ± 1.33	Cullen <i>et al.</i> 2005
Mean AF		2.75	
Pantanal	Telemetry	2.90	Schaller & Crawshaw 1980
Pantanal	Telemetry	4.00	Crawshaw & Quigley 1991
Pantanal	Telemetry/ camera-traps	6.7 ± 1.06	Soisalo & Cavalcanti 2006
Mean Pantanal		4.53	
Amazon	Camera-traps	2.58 ± 1.04	JCF (unpubl. data)
Cerrado	Camera-traps	2.00	Silveira 2004
Caatinga	Camera-traps	2.67 ± 1.06	JCF (unpubl. data)



Fig. 2. Male (right) and female (left) jaguar during mating season on a river bank in the Pantanal (Photo M. Andrews, www.smandrews.com).

ley 1991, Soisalo & Cavalcanti 2006). The seasonal flooding regime concentrates prey species, and consequently predators, in patches of suitable habitat (Crawshaw & Quigley 1991). In addition to the rich natural fauna (Schwartz 2000), cattle present an abundant food source for jaguars (Crawshaw & Quigley 2002). The combination of habitat dynamics, prey availability and cattle density may be responsible for the comparatively high jaguar densities (Soisalo & Cavalcanti 2006).

The lower densities registered for the Atlantic Forest could be attributed to a combination of factors: hunting of jaguars (Crawshaw 1995), competition with humans for food resources (Crawshaw 1995; Leite & Galvão 2002) and the lower carrying capacities of some deciduous and semideciduous habitats present in this biome (Cullen *et al.* 2005, Cullen 2006).

In the Cerrado, the predominantly dry and open vegetation does not present prime jaguar habitat. Again, a less abundant mammal fauna than in the Pantanal (Silveira 2004), also dominated by open vegetation, could reduce carrying capacities for a top predator like the jaguar.

Results from the Brazilian Amazon come from a transitional area between savannas of the Cerrado and Amazonian forests (JCF, unpublished data). Density estimates from the Bolivian Amazon

are similar (2.8/100 km², Silver *et al.* 2004). However, core areas of the Amazon could have higher jaguar densities, considering that the ecotonal study area is under influence of the Cerrado, where jaguar densities are lower.

Finally, the first results from the semi-arid Caatinga biome are higher than expected based on the biome's habitat characteristics and reports of low medium to large sized prey abundance (Oliveira *et al.* 2003). Jaguars were endangered, or at least scarce, in the study area (Serra da Capivara National Park) throughout the previous decade (SMAPR 1994, Wolff 2001). The comparatively actual high jaguar abundance could be explained by an increase of medium and large prey due to an increased patrolling policy in the area, where poaching is common practice (Silveira *et al.*, unpublished data), as well as due to a park-wide system of artificial water holes. This is not the reality in other parts of the Caatinga (T. de Oliveira, pers. comm).

Activity Patterns

Felid activity patterns can be influenced by physical, social, climate and habitat conditions (e.g. Bailey 1993), and for some species including the jaguar, they have been found to coincide with activity of their main prey species (Emmons 1987, Schaller & Crawshaw 1980, Crawshaw & Quigley 1991, Weckel

et al. 2006). Figure 3, based on results from camera trapping studies, shows predominantly a crepuscular-nocturnal activity pattern for the jaguar throughout all biomes where detailed data is available.

In the Atlantic Forest, the species is more active at night than during the day, an activity pattern also exhibited by some of the main prey species (Crawshaw 1995). Considerable daytime activity has also been shown for jaguars in the Amazon and Pantanal (Fig. 3, Schaller & Crawshaw 1980, Crawshaw & Quigley 1991). In the former case, daytime activity could be favored by the dense forest habitat (Silveira 2004). Nocturnal habits of the jaguar in the Cerrado have been confirmed by radiotelemetry studies (Silveira 2004) and repeated camera trapping (JCF, unpubl. data). In this biome, peccaries – one of the main prey species in the study area – showed peaks of activity between 05:01 to 11:59hrs and 19:01 to 04:59hrs (Jácomo 2004), the latter coinciding with the peak of activity for jaguars. Apart from prey activity patterns, extreme climatic conditions like daytime heat in the semi-arid Caatinga may play a role in confining jaguars to a mostly crepuscular-nocturnal activity pattern (Astete 2008).

Habitat Use

Distributed from the south of the United States to the north of Argentina, jaguars are found in many distinct habitat types (Sanderson *et al.*, 2002). Studies on jaguar habitat use in Brazil indicate that although they show a trend to use habitats close to water and with denser vegetation cover, the species uses a large variety of habitat forms:

In the Atlantic Forest, the original vegetation is characterized primarily by ombrophilous and semideciduous forests, but anthropogenic activities have reduced forest cover to 22% of its original extent (MMA 2007a). Here, jaguars were found to strongly select the sparsely available primary and secondary forests and to use dense and open marshland twice as much as its availability (Cullen *et al.* 2005, Cullen 2006). Jaguars also showed avoidance of human-dominated areas such as agriculture and pasture (Cullen 2006). Dense marshes and forest patches possibly enhance the

ability of jaguars to hunt; preference for riparian areas makes them important potential dispersal paths for jaguars (Cullen 2006).

The Pantanal combines influences from neighboring biomes characterized by open (Cerrado, Bolivian Chaco) and closed (Atlantic and Amazon Forest) vegetation with vast open floodplains and marshes (MMA 2007b). In this mosaic landscape, jaguars seem to prefer forested habitats, using gallery forest and forest patches more frequently than expected based on their availability (Schaller & Crawshaw 1980, Crawshaw & Quigley 1991). Even in this water dominated landscape, jaguars are found closer to permanent watercourses than expected by chance (Crawshaw & Quigley 1991).

A similar trend can be observed in the seasonally-flooded Amazon lowlands, where different shrubby and forest habitats occur according to duration and level of flooding. There, jaguars used shrubby low marshlands (*chavascal*) more frequently than other higher and more forested habitat types available, probably because the main prey species are mostly found in this habitat (Ramalho 2006).

The remaining native Cerrado vegetation is dominated by savannah shrub fields, interspersed with areas of forest and open grassland vegetation (MMA 2007c). In the Cerrado, where jaguars have been studied only in one protected area and its surroundings, they showed a preference for arboreal savannah habitat, followed by forest and open grassland (Silveira 2004). Although jaguars have not been recorded in agricultural areas, evidence of the species has been found on cattle pastures (Silveira 2004) and open habitat bordering agricultural matrix (Vynne *et al.* 2007).

Finally, in the Caatinga, characterized primarily by semi-arid steppe-like savannah vegetation forms (MMA 2007d), the only preliminary information comes from a protected area. There, more jaguar records than expected, based on sampling unit distribution, were obtained in extremely dense shrubby Caatinga vegetation, whereas less than expected were obtained in the more open Caatinga. Relative jaguar abundance (photographic rate) showed no correlations with distance to the clos-

est water source (Astete 2008), which is probably due to the Parks' extensive water management system, artificially increasing abundance of this otherwise scarce resource.

Conclusions

Jaguar studies in Brazil are progressively including most aspects of the basic ecology of the species across the biomes where the species occurs. The most common research topic is diet, while jaguar population dynamics remain virtually unstudied. Most studies are concentrated in the Atlantic Forest and the Pantanal, whereas there is still a lack of information in the Amazon, Cerrado and Caatinga. Nevertheless, available knowledge shows jaguars in Brazil to be well adapted to a variety of distinct ecological settings. However, the species' adaptability is limited by its demand for large areas of adequate habitat and a stable prey base. Jaguar ecology in landscapes under human influence are particularly important to better understand these limitations as they provide insight into the species' adaptability, as well as baseline information for landscape scale jaguar conservation efforts.

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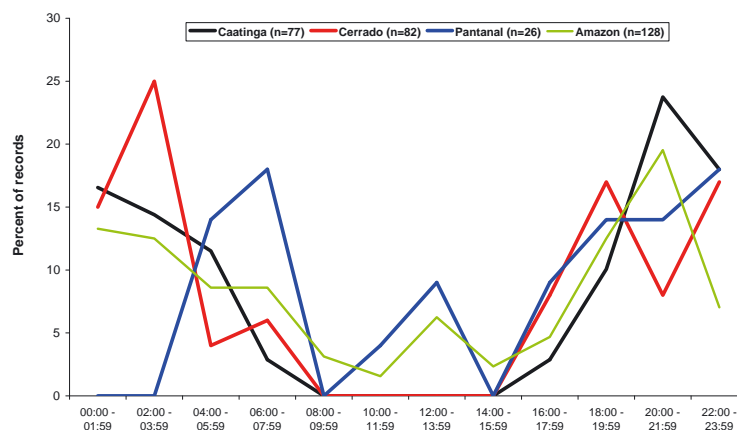


Fig. 3. Jaguar activity pattern expressed as percentage of jaguar records obtained with camera traps in the Amazon, Cerrado, Caatinga and Pantanal (Silveira 2004; Astete 2008; JCF, unpubl. data).

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