Extensive aquatic subsidies lead to territorial breakdown and high density of an apex predator

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Abstract

Energetic subsidies between terrestrial and aquatic ecosystems can strongly influence food webs and population dynamics. Our objective was to study how aquatic subsidies affected jaguar (*Panthera onca*) diet, sociality, and population density in a seasonally flooded protected area in the Brazilian Pantanal. The diet (n = 138 scats) was dominated by fish (46%) and aquatic reptiles (55%), representing the first jaguar population known to feed extensively on fish and to minimally consume mammals (11%). These aquatic subsidies supported the highest jaguar population density estimate to date (12.4 per 100 km²) derived from camera traps (8,065 trap nights) and GPS collars (n = 13). Contrary to their mostly solitary behavior elsewhere, we documented social interactions previously unobserved between same-sex adults including cooperative fishing, co-traveling, and play. Our research demonstrates that aquatic subsidies seen in omnivores can be highly influential to obligate carnivores leading to high population density and altered social structure.

Introduction

Energetic subsidies through the transfer of resources between terrestrial and aquatic ecosystems can strongly influence food webs and population dynamics (Polis, Anderson, & Holt, 1997). The transfer of energy from large emergences of aquatic insects to terrestrial systems is the canonical example of this phenomenon (Nakano & Murakami, 2001), but fish-consuming terrestrial vertebrates can also play an important role. Salmon systems famously support hyperabundant bear (*Ursus arctos*) populations with modified social dynamics due to the need to tolerate conspecifics at the point sources (e.g., waterfalls) and linear features (e.g., streams) where salmon become accessible (Egbert & Stokes, 1974; Gende & Quinn, 2004). Similarly, Rose and Polis (2016) found coastal coyote (*Canis latrans*) populations subsidized by marine resources to be on average 4-5 times more abundant than inland populations. Several other omnivorous terrestrial carnivores forage in marine or freshwater systems such as gray

wolves (*Canis lupus*) (Darimont, Paquet, & Reimchen, 2008), raccoons (*Procyon lotor*) (Carlton & Hodder, 2003) and arctic foxes (*Vulpes lagopus*) (Roth, 2002), but aquatic subsidies in obligate terrestrial carnivores are thought to be rare. Of the obligate carnivores, jaguars (*Panthera onca*) have been most frequently linked to aquatic resources such as caiman and chelonians (Escobar-Lasso et al., 2016; Guilder, Barca, Arroyo-Arce, Gramajo, & Salom-Pérez, 2015; Silveira, Ramalho, Thorbjarnarson, & Magnusson, 2010), although terrestrial mammals still dominate their diet.

A resource-rich environment may enable multiple individuals to share a common resource, which typically results in higher animal densities (Newsome, Ballard, Dickman, Fleming, & Ven, 2013), smaller home-ranges and increased social interactions among individuals according to the resource dispersion hypothesis (Macdonald, 1983). Most large felids, including the jaguar, are considered solitary species with social interactions generally limited to courtship and territorial disputes (Sunquist and Sunquist 2002; Kleinman & Eisenberg 1973). However, the degree of intraspecific tolerance and sociality can change with resource availability (Elbroch, 2017; Elbroch & Quigley, 2017). The Pantanal wetlands in central South America harbors abundant terrestrial and aquatic jaguar prey resources. Here, jaguars reach high population densities (Soisalo & Cavalcanti, 2006) and use smaller home-ranges than elsewhere in their range (Morato et al., 2016), but spatial tolerance of conspecifics, defined by overlapping home-ranges, seem to vary. Azevedo and Murray (2007) found that jaguars maintained exclusive territories while Cavalcanti and Gese (2009) found extensive overlap among males but not among females. Consumption of aquatic prey, mainly caiman (*Caiman yacare*), varies among study areas from approximately 20% (Azevedo and Murray 2007; Cavalcanti and Gese 2010) to 30% (Perilli, Lima, Rodrigues, & Cavalcanti, 2016) with terrestrial mammals still constituting the majority of the diet in all prior research. In addition, domestic cattle are abundant and make up a considerable portion of the jaguar diet in the southern Pantanal where most research has been conducted to date. Thus, it is currently unclear whether aquatic subsidies have altered the abundance or social structure of these jaguar populations, as has been demonstrated with other omnivorous carnivores.

In contrast to the southern Pantanal, the ecology of jaguars in the wetter northern portion (i.e., within the Brazilian state of Mato Grosso) remains largely unstudied. Taiamã Ecological Station (hereafter, Taiamã), a small and seasonally flooded protected area (115.55 km^2), was suggested to have an unusually high jaguar density based on frequent jaguar sightings (Kantek & Onuma, 2013). A large presence of jaguars in this area is further made obvious by abundant jaguar footprints, scats, scratch marks on trees and large caiman carcasses scattered along the river margins (this study). Taiamã (16°50' S and 57°35' W, Figure 1) was established in 1981 to protect this unique wetland ecosystem and its high diversity and abundance of fish species (ICMBIO 2017). Importantly, there are no human settlements or cattle ranching within or in the immediate vicinities of Taiamã and fishing is strictly prohibited (ICMBIO 2017). Our objectives were to study the ecology of jaguars at Taiamã to determine if the presence of abundant aquatic resources affect their diet, social behavior and ultimately population density, and to place these findings in the context of previous literature on jaguar ecology. To accomplish these objectives, we collected jaguar scats for dietary analysis, estimated jaguar density and documented social interactions using camera traps and telemetry data from 13 jaguars. This research details a rare example of how allochthonous resource subsidies can be so prolific that they influence the behavior and social organization of an apex predator.

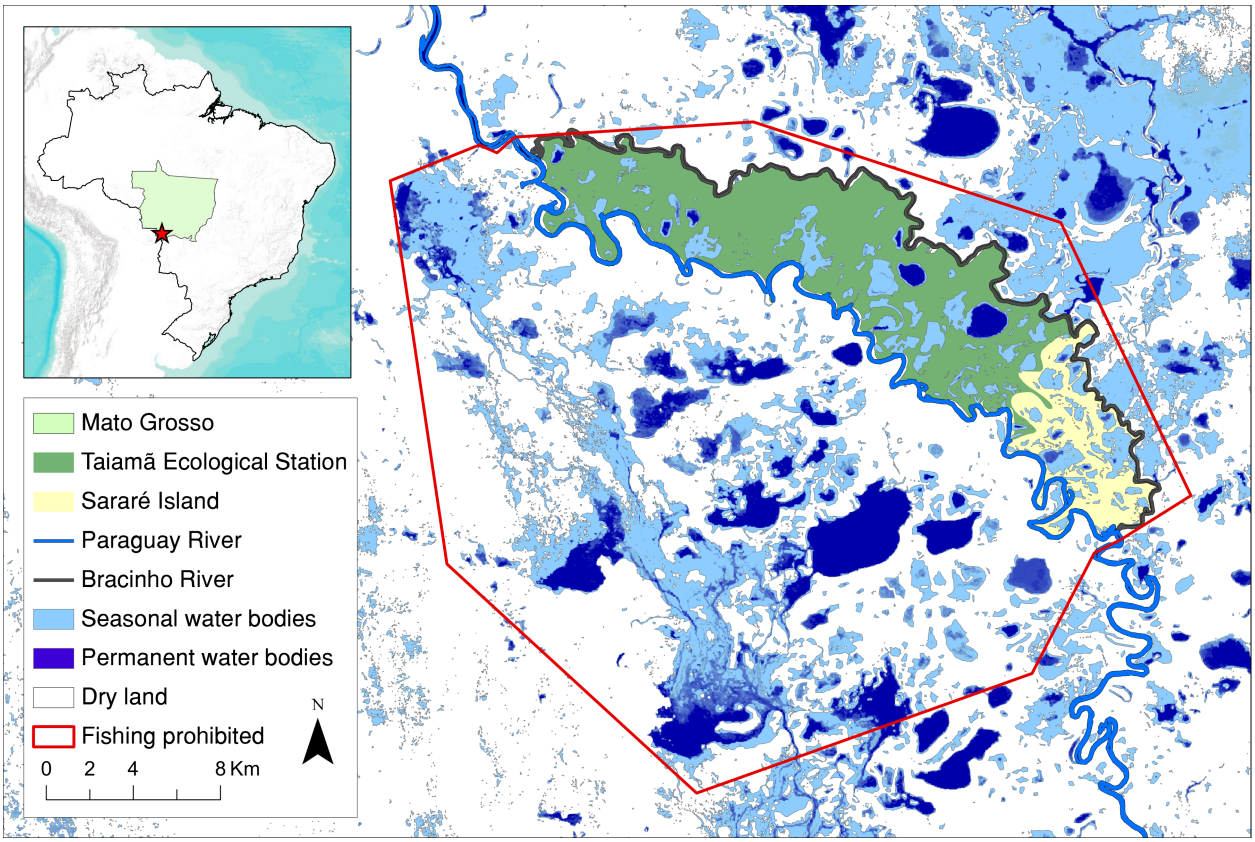

Figure 1 Study area. Map of study area at Taiamã Ecological Station within the Pantanal wetlands in Mato Grosso, Brazil.

Results

In total we operated 59 camera stations for 8,065 days between 2014 and 2018 (Table 1; Figure 2). Jaguars were detected in 95% of the cameras (n = 56) and were the most frequently detected mammal (Figure 3). We obtained 1,594 videos of jaguars (excluding the photos from the paired cameras in 2018), representing 385 individual weekly detections with the number of detections per individual ranging from one to 34 (mean 5.6 ± 5.9 SD). We detected 12 out of the 13 telemetered jaguars with our camera traps. We detected an additional 29 females, 21 males, two individuals of unknown sex, and four cubs, representing a total of 69 unique individuals. The maximum number of unique jaguars captured by one camera was 15 across all 3 years including 9 just in 2015. Both right and left flanks were obtained for

most of the individuals, despite our unpaired camera setup in 2014 and 2015. Only one jaguar was captured only on her left side but was still included in the dataset since the closest female with only a right-side capture was detected 20 km away and had a completely different rosette pattern type. We were therefore able to retain all identified jaguars in the analyses. The highest minimum number of jaguars known to be present within the study area within one camera session was 40 (Table 1).

Table 1. Camera trapping summary statistics. M = male, F= female, U = unknown sex, C = cub. [1]Capture defined as an individual per camera-trap per occasion. [2]Number of jaguars known to be present in the study area based on telemetry or camera detections.

Camera session	1 (Aug-Oct 2014)	2 (Mar-Jun 2015)	3 (Jul-Nov 2015)	4 (Aug-Oct 2018)
Length	56	126	126	65
Season	Dry	Wet	Dry	Dry
Camera days	2069	2125	2366	1271
Camera stations	39	20	24	20
Captures[1]	108	165	183	135
Unique individuals	26 (13M, 12F, 1U)	33 (15M, 16F, 1U, 1C)	28 (17M, 10F, 1C)	25 (8M, 14F, 3C)
GPS-collared	8 (5M, 3F)	6 (4M, 2F)	4 (2M, 2F)	0
Min known to be alive[2]	31	40	31	27

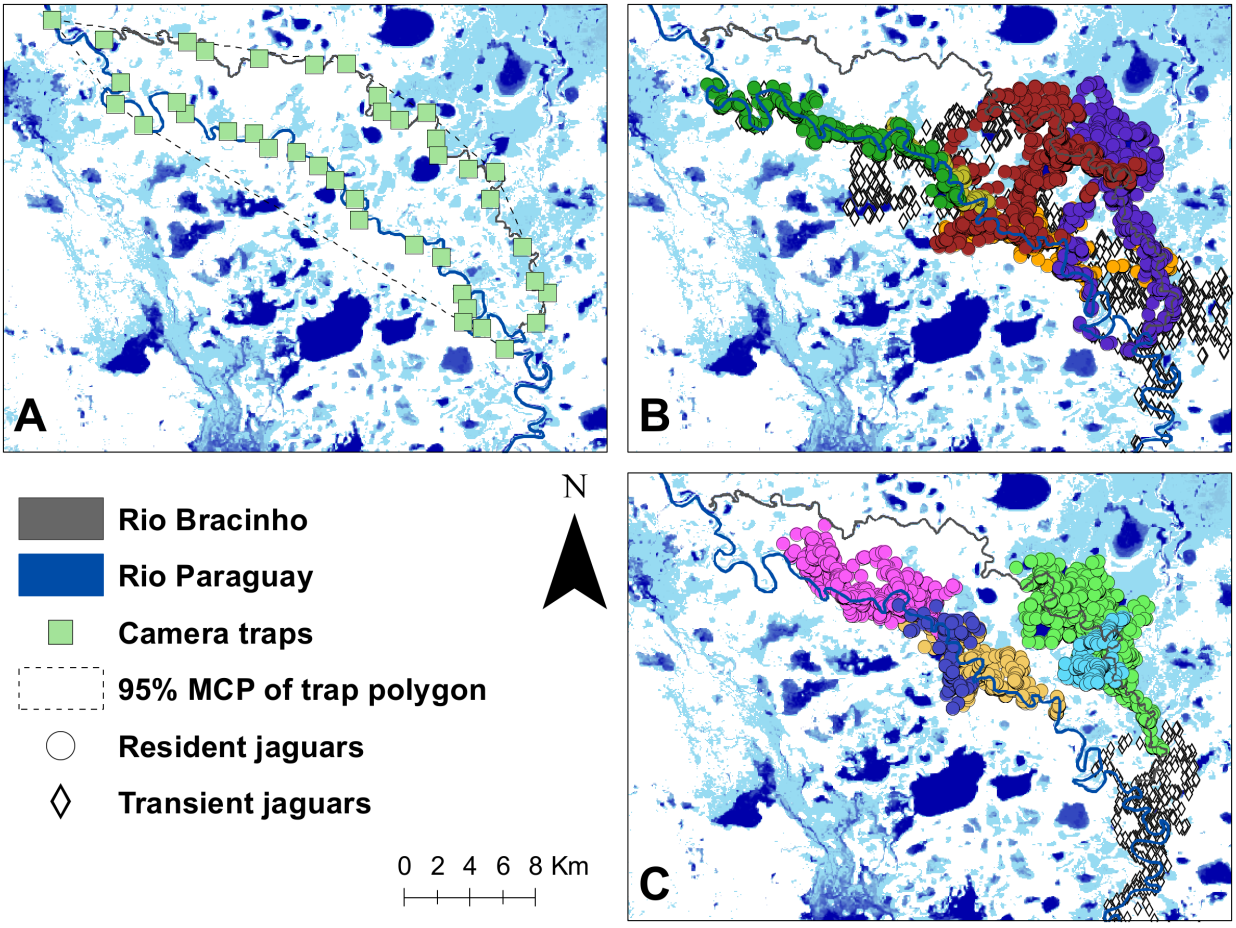

Figure 2 and Supplemental Animation. Camera trap locations and jaguar movement at Taiamã Ecological Station. A) Camera trap placement along the Paraguay and Bracinho rivers. B) GPS locations of six resident males and one transient. C) GPS locations of five resident females and one transient

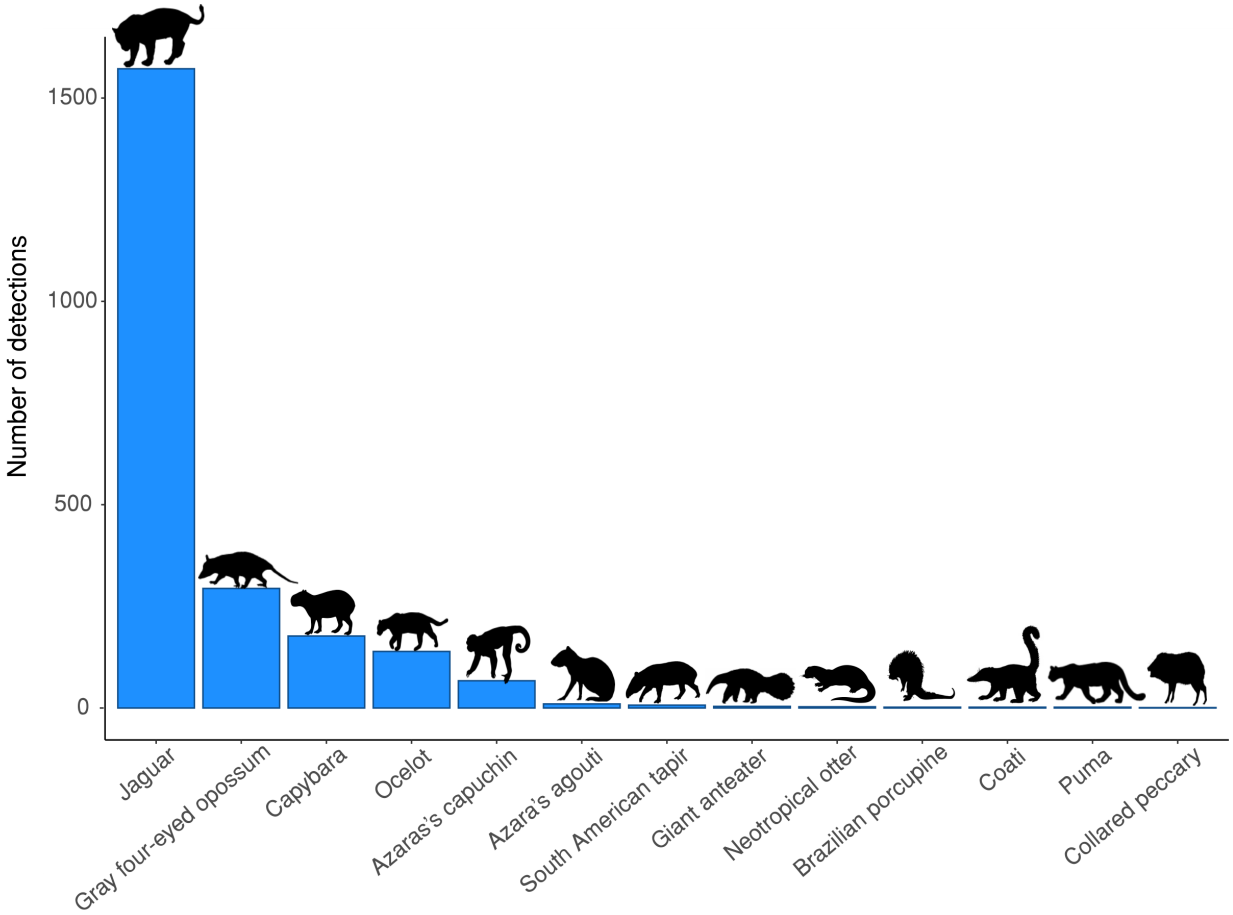

Figure 3 Total number of mammal detections. Number of detections of medium and large mammal species at Taiamã Ecological Station using camera traps from 2014-2018.

The telemetered jaguars spent on average 96% of the time within the study area (Table 2; Figure 2). Estimated jaguar density was 12.4 per 100 km² and mean capture probability per weekly occasion was 0.18 (0.15 - 0.21 Bayesian Credible Interval; BCI) for females and 0.27 (0.24 - 0.31 BCI) for males. Density was similar across the three dry season sessions at 12.3 (10.1 - 14.4), 11.9 (10.1 - 12.9) and 11.3 (9.4 - 13.1) jaguars per 100 km², in session 1, 3, and 4, respectively. The wet season estimate from session 2 was 14.3 (12.2 - 15.4) jaguars per 100 km² (Table 2), even though some 40% of the Taiamã land area becomes seasonally flooded.

Table 2 Model parameter estimates of the posterior distributions for jaguar density per 100 km² and detection parameters in Taiamã Ecological Station across four camera trapping sessions. $\tilde{p}$ is the fraction of time jaguars spent within the bounds of the trapping area as estimated by telemetry data and p is the probability of detection within a weekly occasion.

Parameter	Mean	2.50%	50%	97.50%
Session 1 (Aug-Oct 2014)	12.28	10.13	12.26	14.43
Session 2 (Mar-Jun 2015)	14.30	12.20	14.47	15.41
Session 3 (Jul-Nov 2015)	11.90	10.12	12.02	12.95
Session 4 (Aug-Oct 2018)	11.26	9.36	11.26	13.05
$\tilde{p}$	0.96	0.82	0.97	1.00
p-females	0.18	0.15	0.18	0.21
p-males	0.27	0.24	0.27	0.31

Jaguar diet

We identified nine prey items in 138 jaguar scats collected from 2013-2018. The jaguar diet was dominated by three taxonomic groups: reptiles (55%), fish (46%) and mammals (11%) (Figure 4A). These findings were corroborated by camera data showing jaguars feeding on fish and caimans, and other field observations such as large caiman skulls and fish carcasses scattered along the rivers. Fish remains found in the scats could not be identified to species, however, the camera data revealed jaguars capturing several types of fish such as thorny catfish (*Doradidae*) (Figure 4D), pacu (*Piaractus mesopotamicus*), red-bellied piranha (*Pygocentrus nattereri*), and large tiger catfish (*Pseudoplatystoma fasciatum*) (Figure 4C). Most mammals consumed were semi-aquatic (i.e., capybaras; 7%) (Figure 4B). Rare prey items included green iguana (*Iguana iguana*), Brazilian porcupine (*Coendou prehensilis*), freshwater crab, and gray four-eyed opossum (*Philander opossum*) (Figure 4B). The high frequency of occurrence of fish and reptiles in the scats found a Taiamã was unparalleled with other studies throughout the jaguar's range (Figure 5). Jaguars foraged for fish mainly by searching while walking slowly through the water (Figure 6 A, B) and attacking rapidly when spotting a fish (Figure 6, C). Jaguars also looked for fish while sitting still in the water (Figure 6, D).

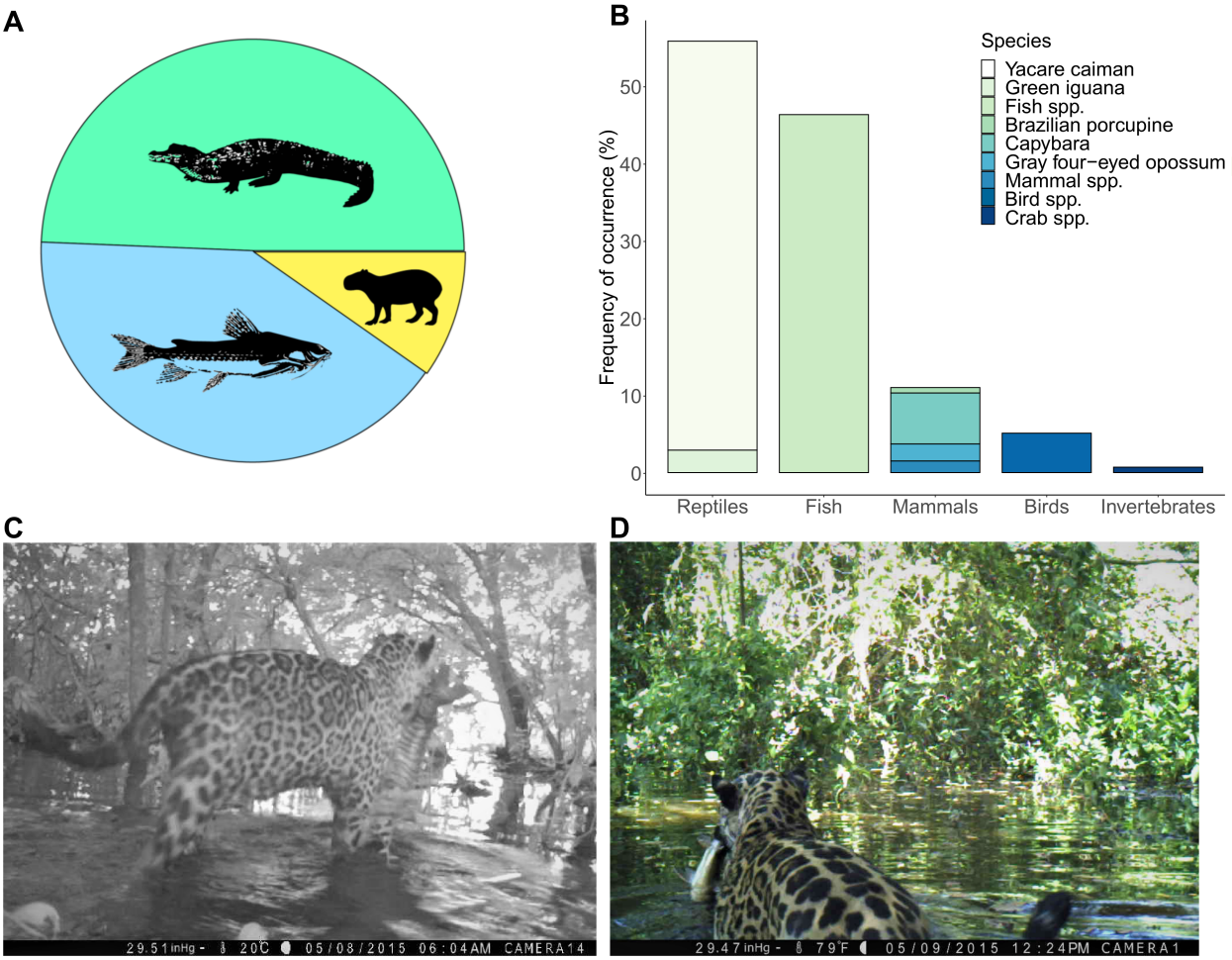

Figure 4 Relative percentage of occurrence of prey items found in jaguar scats (n = 138) in Taiamã Ecological Station between 2013 and 2018. (A) Main food groups: reptiles, fish, and mammals. (B) All identified prey items. (C) F8 carrying a tiger catfish (*Pseudoplatystoma fasciatum*). (D) M4 after catching a thorny catfish (*Doradidae* spp.).

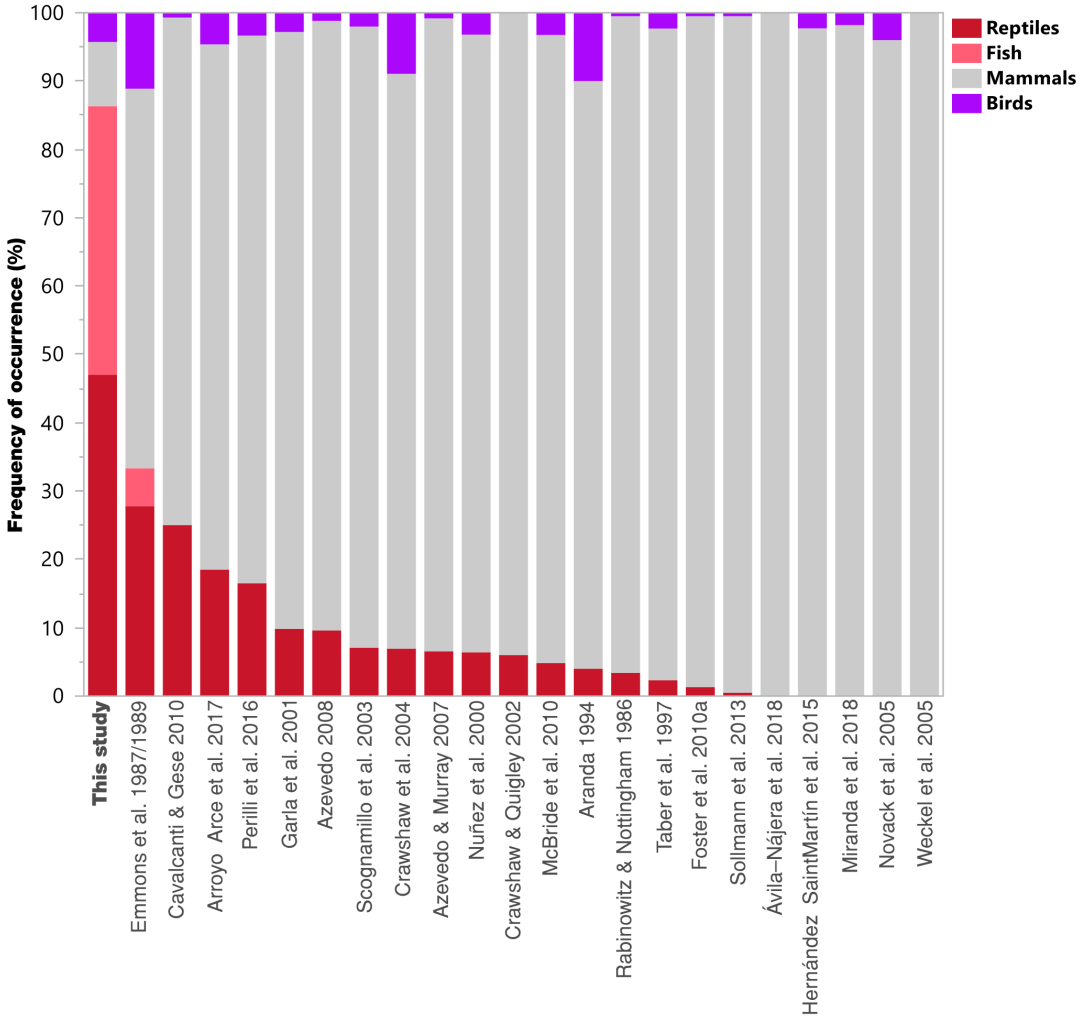

Figure 5. Frequency of occurrence of major vertebrate prey taxa (mammals, reptiles, fish, and birds) found in jaguar diets documented by different studies throughout the geographic range of jaguars. Only peer-reviewed studies with a sample size of at least 20 scats or kill sites were included. See Supplementary file 3 for more information on sample sizes and study locations.

Figure 6. Videos of jaguar fishing behavior. A) Mother and cub searching for fish together, B) Jaguar looking for fish by walking slowly through water, C) Failed capturing attempt, D) 'Sit and wait' foraging technique.

Social interactions

All resident GPS-collared males had overlapping 95% AKDE home ranges, except for M3 and M4 (Figure 7A). M1 overlapped from 17.6 to 25.5% with M2 and M3, respectively, while M2 and M3's home ranges overlapped by 64.7%. M5 overlapped with M1 by 7.6% and 16.1% with M3. The 95% AKDE home range also overlapped extensively between GPS-collared females (Figure 7B). F2's home range overlapped by 58.6% with F1 and the home ranges of F3 and F4 overlapped to 21.6%. F1 and F2 were unrelated while F3 and F4 were mother and daughter (D.L.Z Kantek, personal communication, January 2021). Since these home range overlap estimates were exclusively derived from telemetered individuals, they fail to account for spatial overlap with uncollared jaguars. Approximately 4-15 jaguars (including collared and uncollared) were detected with the cameras overlapping each home range.

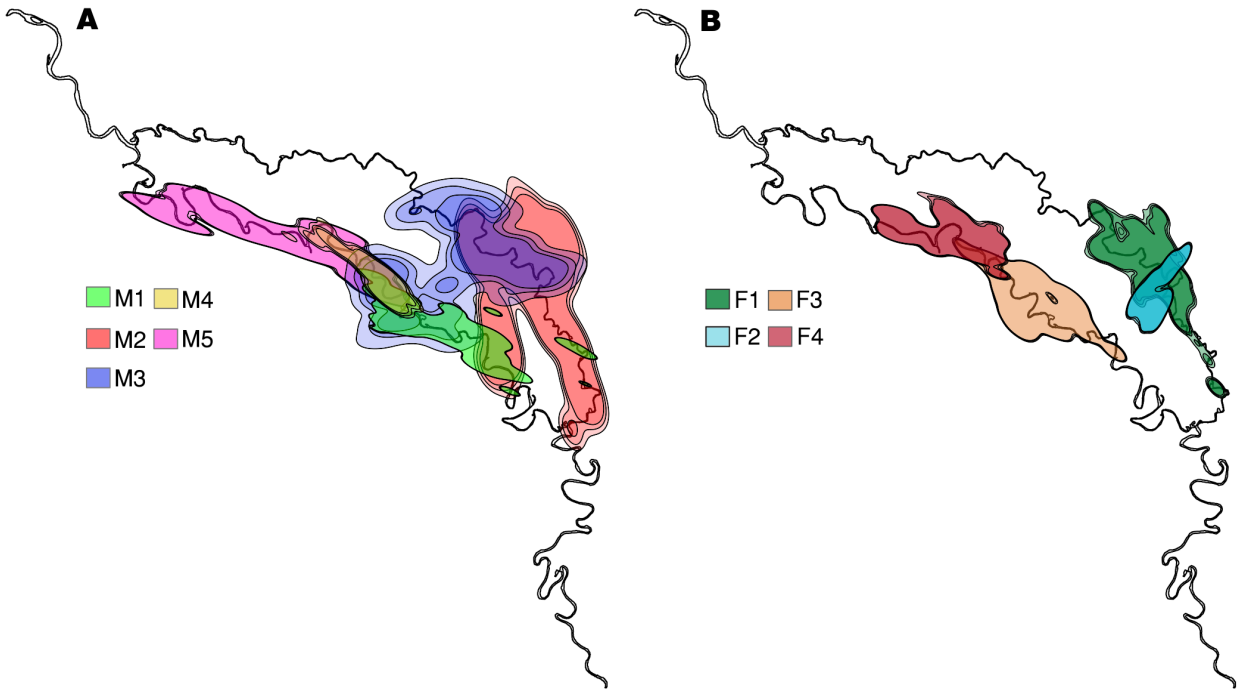

Figure 7. 95% AKDE home ranges for resident jaguars GPS-collared at Taiamã Ecological Station between 2014-2015. A) Five male jaguars, and B) 4 female jaguars.

We documented 80 independent social interactions between adult jaguars based on the camera (n=40) and GPS data (n=40). The majority of the interactions were between males and females (M-F 85%), often displaying courtship behavior (Figure 8B and C) throughout the wet and dry seasons. The M-F interactions involved 29 individual jaguars (14 males and 15 females). One male and female mated with each other both in 2015 and 2018. We documented 12 interactions of the same sex (one F-F and 11 M-M) consisting of 10 individuals (two females and eight males). Two GPS-collared males, M2 and M1, moved continuously within approximately 41-182 m of each other for two days. Eight months later the same two males were captured with the same camera 5 min apart. M2 moved continuously with another GPS-collared male (M3) for 10 hours within 4-38 m of each other, again two days later (2 hours; 14 m apart) and were close again two weeks later (1 hour; 159 m). None of the three males were related (D.L.Z Kantek, personal communication, January 2021). Two other males (M7 and M21) were seen fishing together (Figure 8D) and walking past another camera together one month later. Two males (M29 and

M27) spent 30 min in front of a camera "playing" (Figure 8E and F). Two females (F2 and F4) were documented in the same location 12 min apart (Figure 8G). We lack information on potential relatedness among the interacting uncollared jaguars.

A

Type of interaction	Number of camera interactions	Number of GPS interactions	Photo
Female + male	33	35	B, C
Male + male	6	5	D, E, F
Female + female	1	0	G

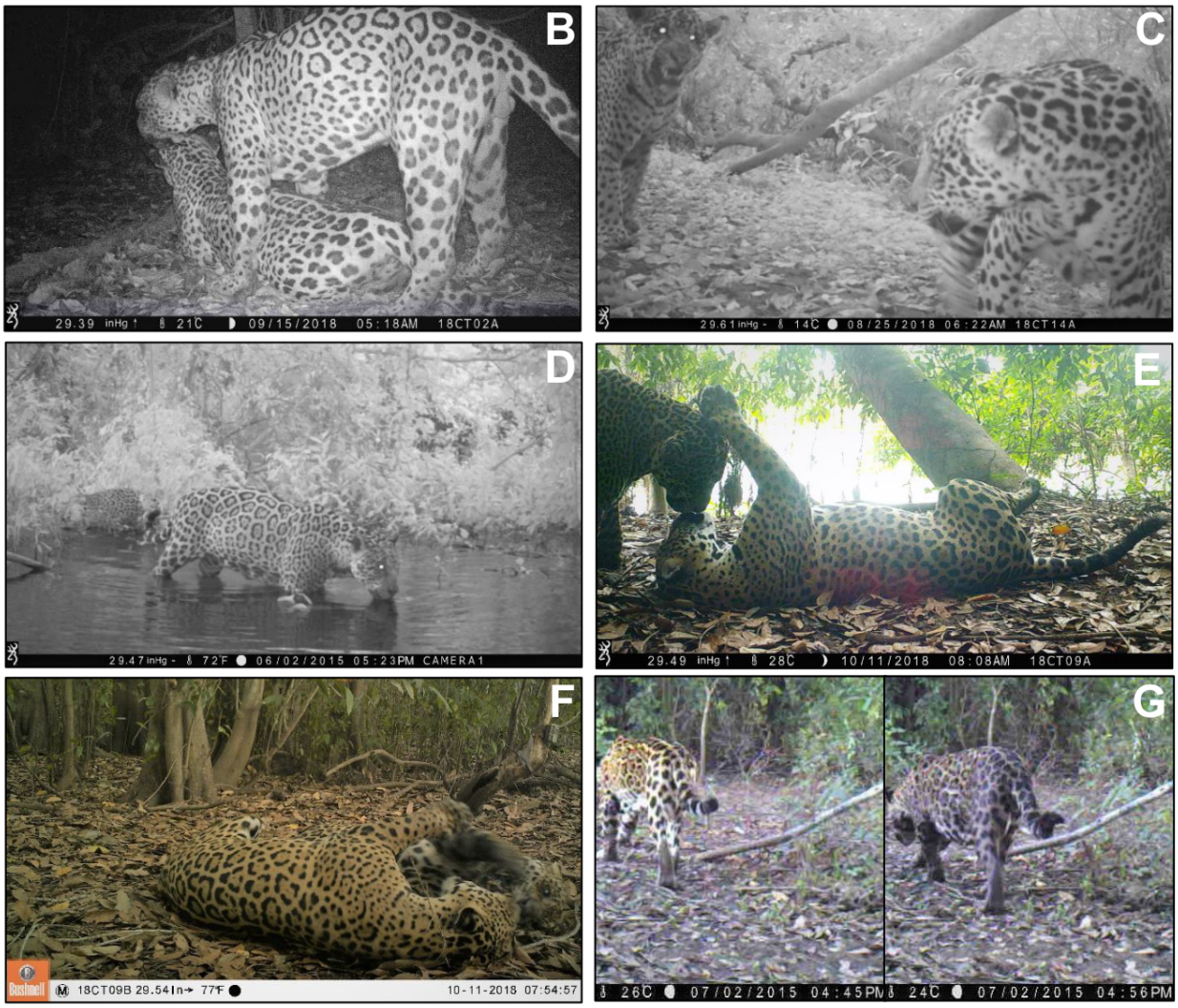

Figure 8. (A) Number and type of social interactions among adult jaguars determined by GPS data and camera trap data. (B-C) Male (M5) and female (F4) mating behavior, (D) Two adult males (M7 and M21) fishing together, (E-F) two adult males (M29 and M27) playing, (G) Two females (F2 and F4) captured with the same camera 12 minutes apart.

Discussion

With a density of 12.4 jaguars per 100 km², our results indicate that Taiamã is home to the highest density jaguar population described to date. Other high jaguar density estimates using spatial-capture recapture analysis include 4.4-4.5 jaguars/100 km² from the Peruvian Amazon (Tobler et al., 2013; Tobler et al., 2018) and 4.4 jaguars/100 km² in the Venezuelan Llanos (Jędrzejewski et al., 2017). Our density estimate using SCR was 6.0 jaguars per 100 km² (Supplementary file 2), but as discussed previously, this is an underestimate due to the elongated home ranges of jaguars at Taiamã (Figure 2). As a very minimum estimate, using just our 13 *telemetered* individuals, which we knew were all present in 2015, with on average 96% of GPS locations contained within the boundaries of our study area (236.7 km²), would suggest a density of approximately 5.4 jaguars per 100 km², without considering the additional 56 individuals detected with cameras.

Reptile consumption by jaguars at Taiamã was also the highest observed to date (Figure 5) although they can be a common component of jaguar diets in seasonally flooded habitats (Cavalcanti and Gese 2010; Azevedo and Verdade 2012; Silveira et al. 2010). This is particularly the case in the flooded *várzea* forests of the Amazon where common terrestrial mammalian prey are absent during the flood pulse (Silveira et al., 2010). However, the heavy reliance on fish appears unique to the jaguars at Taiamã and has been rarely documented in the literature (Figure 5) despite jaguars being commonly associated with rivers and waterbodies (Morato et al. 2018; Kanda et al. 2019). Prior to the extensive fish consumption observed here, the only records include anecdotal observations of jaguars fishing summarized in Gudger (1946) and more recently Emmons (1987) found fish in two jaguar scats. Other felids living in semi-aquatic habitats such as tigers (*Panthera tigris*) in the Sundarbans still consume mostly terrestrial mammals (Aziz, Islam, & Groombridge, 2020). The fishing cat (*Prionailurus viverrinus*) may be the most similar example of a piscivorous felid akin to the jaguars at Taiamã (Ganguly & Adhya, 2020).

228 Ecological theory would predict that a high density of an apex predator, subsidized by
229 allochthonous resources, would have consequences for the surrounding community through modification
230 of top-down forces (Leroux & Loreau, 2008). It is unclear whether this exceptionally high abundance of
231 jaguars, an opportunist predator supported by abundant aquatic resources, has had a negative impact on
232 the terrestrial mammal community at Taiamã. Common terrestrial mammalian prey for jaguars such as
233 capybara, tapirs, peccaries (*Tayassuidae*), giant anteater, and marsh deer (Emmons, 1987; Novack, Main,
234 Sunquist, & Labisky, 2005; Weckel, Giuliano, & Silver, 2006) are present at Taiamã (De Lázari et al.
235 2013; Mauro et al. 1998), yet mammals were only found in 11% of the scats. The seasonally flooded
236 landscape at Taiamã may play a stronger role in determining the abundance and distribution of terrestrial
237 species (De Lázari et al., 2013). For example, mammals that are suited to aquatic life such as capybaras
238 are common, but rarely feature in the diet of these jaguars. It is possible that the abundance of aquatic
239 resources has resulted in a highly specialized jaguar diet, potentially benefitting the terrestrial community
240 through apparent mutualism (Holt & Bonsall, 2017) and provisioning of carcasses (Escobar-Lasso et al.,
241 2016). However, even if jaguars only occasionally take certain terrestrial prey, they may still suppress
242 those species due to the large number of jaguars.

243 Jaguars at Taiamã may have adapted their social system in response to abundant prey resources,
244 similar to how brown bears are more tolerant of conspecifics during periods of high salmon abundance
245 (Egbert & Stokes, 1974). According to optimal foraging theory, individuals widen their dietary niche by
246 switching to alternative food sources to avoid competition when food is limited. When food is abundant,
247 individual prey selectivity increases and the diversity of prey taken decreases (MacArthur and Pianka
248 1966). The almost complete dominance of just two vertebrate taxa — fish and caiman — in the diet of
249 jaguars at Taiamã further suggests food is abundant and intraspecific competition is relaxed. Home-range
250 overlap among jaguars, in particular males, has been documented to varying degrees in other areas, but
251 may not be an indication of social tolerance since individuals may still avoid each other temporally
252 through the use of scent and scrape marking (Harmsen, Foster, Gutierrez, Marin, & Doncaster, 2010) or

253 vocalizations. Outside of male and female courtship behavior, camera-trapping observations of adult
254 jaguars together, simultaneous GPS locations and/or direct observations are exceedingly rare in the
255 literature. Schaller and Crawshaw (1980) described an incident where a jaguar hunter saw three males
256 courting one female at the same time. Cavalcanti and Gese (2009) found two males sharing a carcass
257 together and two other males moving within 200 m of each other on three occasions. Our GPS data
258 revealed one male spending several hours, sometimes days within 200 m of two other males and our
259 cameras detected another two males walking and fishing together. In addition, the overlapping home-
260 ranges of a pair of females and the detection of a female followed by another female 12 min later, suggest
261 that jaguars can be more social than previously thought. Jaguars may share kills with offspring, mates or
262 even same-sex individuals (Cavalcanti & Gese, 2009), but observations of jaguars hunting together have
263 not, to our knowledge, been published previously. In addition to the two adult males mentioned earlier, a
264 female and her older cub were frequently observed fishing together (Figure 6, B). We cannot determine
265 whether this form of cooperative fishing improved fish capture efficiency, or whether the jaguars just
266 tolerated the close proximity of each other without deriving any prey-acquisition benefits.

267 Further indication that high resource abundance at Taiamã affects the social organization of
268 jaguars comes from clear evidence of social play which in animals is thought to occur when all biological
269 needs have been met (Bekoff, 1972). The incident of play between M27 and M29 started with passive
270 submissive patterns such as rolling over, facial rub, and face-paws (Bekoff, 1972). The play then
271 transitioned to play-fighting with wrestling, soft bites, and mounting. Play in juvenile mammals is
272 essential for behavioral development but play among adults is rarely described and its motivations are
273 more difficult to interpret. Latour (1981) suggested adult play in male polar bears was used to practice
274 and enhance social skills for future agonistic interactions. While our results indicate an increased social
275 tolerance among jaguars at Taiamã, some males displayed typical territorial behavior such as urine
276 spraying, scraping and roaring, suggesting that intraspecific social behavior is a complex phenomenon
277 that demands further investigation.

Conclusion

Our study demonstrates that aquatic subsidies, frequently described in omnivores, can be common in obligate carnivores as well. Whether our results are generalizable to other jaguar populations in seasonally flooded habitats is confounded by the presence of domestic cattle, another subsidy, in other areas. The flooded nature of the landscape surrounding Taiamã has largely prevented the expansion of cattle farming, yet this region faces many threats and efforts to increase protected areas are critically needed to ensure future persistence of jaguars in the area (Cardoso et al., 2019; Quigley & Crawshaw, 1992). In an effort to prioritize conservation efforts throughout the jaguar's distribution, Sanderson et al. (2002) stated "the goal is not to determine the most important site for jaguar conservation overall, or the most important site in a given country, but rather to find the most important sites for ecologically distinct populations of jaguars". In this study we have provided evidence that Taiamã is a stronghold for jaguars, but also revealed aspects of jaguar ecology that are rare elsewhere; an extensive piscivorous diet facilitating an extremely dense population with a more fluid social structure characterized by high levels of individual tolerance. This work further sheds new light on the relationship between carnivore socioecology and prey abundance and distribution, showing that the modal pattern of solitary hunting observed in the vast majority of hyper-carnivores can be broken given the nature, productivity and distribution of the resource base. Future research is needed to understand the role jaguars play linking aquatic and terrestrial food webs and the implications of this highly subsidized population on the surrounding community.

Materials and methods

Study Area

The study area encompassed Taiamã Island and contiguous Sararé Island bounded by the Paraguay and Bracinho rivers (Figure 1). The area is characterized by seasonally flooded grasslands with numerous seasonal and permanent lakes and riparian gallery forests growing along the rivers. The climate is defined by a dry (April-September) and wet season (October-March) with an average annual precipitation of 1,200-1,300 mm (Mamede & Alho, 2006). The maximum river level occurs between February-June and the lowest in August-November. The fluctuating water levels substantially alter the availability of terrestrial vs aquatic habitats (Figure 1) and determine local ecological patterns and processes, including the distribution and abundance of wildlife (Alho, 2008; Desbiez, Bodmer, & Tomas, 2010). In addition to jaguars, the reserve supports several other vertebrates well-adapted to water, most notably caimans (*Caiman yacare*) and capybaras (*Hydrochoerus hydrochaeris*). Other known jaguar prey species present include giant anteaters (*Myrmecophaga tridactyla*), Brazilian tapir (*Tapirus terrestris*), marsh deer (*Blastocerus dichotomus*), and Brazilian porcupine (*Coendou prehensilis*) (De Lázari et al. 2013; Mauro et al. 1998; this study).

Camera dataset

We carried out three camera trapping surveys between 2014 and 2018. The absence of roads or trails coupled with the prolonged flood pulse of the landscape and the high jaguar density presented unique logistical challenges for field work and prevented any movement by car or foot. All camera deployments were therefore boat-based and restricted to the major waterways and, thus, prevented the use of a systematic camera grid. We used unbaited Bushnell (Trophy Cam 119636, Overland Park, Kansas) and Browning (Dark Ops BTC-6, Birmingham, AL) camera traps separated by approximately 2 km along the Paraguay and Bracinho rivers. The two waterways were parallel to each other and separated by 4-6 km (Figure 1). Camera availability varied across the years resulting in 39 and 27 single cameras used in 2014

326 and 2015, respectively. In 2018 each camera station consisted of two paired cameras (20 stations in total).
327 In 2014 and 2015 the cameras were set to video mode (20 sec/video) and operated for 56 (August-
328 October) and 252 days (March-November), respectively. In 2018 one camera was set to video and the
329 other paired camera was set to take photos (three per burst) for 65 days (August-October). Cameras were
330 set approximately 50 cm off the ground on trees with batteries and SD cards checked every three weeks.
331 The study area encompassed an area of approximately 236.7 km², which is larger than a jaguar home
332 range in this area (Morato et al., 2016) as recommended for accurate density estimation (Tobler & Powell,
333 2013). Individual jaguars were identified in each photo or video based on their unique coat patterns. The
334 camera detections were collapsed into weekly occasions for density estimation. The 252-day long camera
335 deployment in 2015 was split into two sessions to assume demographic closure resulting in four sessions
336 of 8, 18, 18 and 10 weekly occasions each. Camera trap sampling details are summarized in Table 1.

337

338 *Telemetry dataset*

339 Seven male and six female jaguars were captured between December 2011 and April 2016 as part of
340 concurrent studies (Morato et al. 2016; Miyazaki et al., 2016; Cardoso et al., 2020) approved by Instituto
341 Chico Mendes de Conservação da Biodiversidade (SISBIO number 30896-3). The jaguars were captured
342 using foot snares and immobilized with tiletamine and zolazepam (10 mg/kg). Two of the jaguars were
343 fitted with VHF radio-collars and the remaining (n = 11) were fitted with Lotek-Iridium GPS collars
344 (Lotek Wireless, Newmarket, Canada) programmed to record location data every hour and to
345 automatically drop-off the animal after 400 days.

346 *Density estimation*

347 A fundamental issue with density estimation is how to deal with a lack of geographic closure given that
348 some fraction of detected individuals primarily lives outside the study area. Capture-recapture models
349 (CR; Otis et al. 1978) estimate abundance and derive density by dividing the number of individuals by the

effective sampling area. However, the effective sampling area is imprecisely estimated using a buffer strip around the study area of either the full Mean Maximum Distance Moved (MMDM) or ½ MMDM from the capture data, which are considered as a surrogate for home range diameter or radius. Thus capture-recapture models can be sensitive to arbitrarily defined effective sampling area. In the past decade, Spatially explicit Capture-Recapture models (SCR; Borchers and Efford 2008; Royle and Young 2008) have become a preferred method for density estimation over conventional non-spatial capture-recapture techniques. SCR models solve the geographic closure problem by incorporating the spatial location of detections to estimate the activity center of each animal, and the density of activity centers is then treated as the population density.

While SCR models present a useful advance over conventional CR models, they assume isotropic (i.e. circular) home ranges such that detection probability of each individual falls off equally with distance from its activity center. Our telemetry data revealed that the direction of jaguar movement at Taiamã follows the rivers closely and the home ranges are therefore elongated and highly anisotropic (Figure 2). In such a situation, SCR models may still perform well if sufficient detectors are placed in two dimensions capturing both the major axis of movement (along the rivers in our case) and the minor axis (perpendicular to the rivers) (Efford, 2019). The bias can then be corrected by applying anisotropic detection models (Murphy et al., 2016). Since our camera deployment was boat-based and therefore restricted to the rivers surrounding Taiamã island, we were unable to effectively capture jaguar movement in the minor axis. Further, the telemetered jaguars did not uniformly share the same home range orientation (Figure 2) which is necessary to fit anisotropic detection models. Applying a SCR model to this unusual dataset where the detectors are aligned with elongated animal home ranges would therefore lead to an overestimation of the spatial scale parameter and consequently underestimate density (Efford, 2019).

For data-rich applications where a representative portion of the population has been telemetered, the extent of geographic closure violations can be corrected for directly (Ivan et al. 2013a, 2013b) to

375 estimate population density without the restrictive assumptions of circular home ranges or the size of the
376 effective sampling area. This method uses a conventional Huggins closed-capture model augmented by
377 telemetry data. The study area is first determined by applying a minimum convex hull around the
378 detectors. Crucially, rather than assuming each captured individual is fully present within the study area
379 such as in a standard CR model (1 in the equation 1 numerator) (i.e., the study area is geographically
380 closed) (eq. 1), residency ($\tilde{p}$) is instead used by estimating the proportion of time the telemetered
381 individuals spend within the area (eq. 2). p_i is the detection probability for individual *i*, M_{t+1} is the total
382 number of animals detected, and *t* is the number of occasions.

383 $$N = \sum_{i=1}^{Mt+1} \left(\frac{1}{p_i}\right) \quad (1)$$

384 $$N = \sum_{i=1}^{Mt+1} \left(\frac{\tilde{p}}{p_i}\right) \quad (2)$$

385 We estimated jaguar abundance (*N*) allowing for variation in capture probability (p) between males and
386 females as recommended by Sollmann et al. (2011). We used telemetry data to estimate $\tilde{p}$ as the grand
387 mean among individuals of the Binomial probability parameter in a model for the number of telemetry
388 points inside the study area relative to outside. We included a random intercept in the logit-linear model
389 for $\tilde{p}$ so that one individual's data would not dominate the estimate. Density was then estimated by
390 correcting *N* with $\tilde{p}$ (Eq. 2) and then dividing by the study area. All models were implemented in JAGS
391 (Plummer, 2003) accessed through the R package JagsUI (Kellner, 2019). Code is available in
392 Supplementary file 1.

393

394 *Diet analysis*

395 Jaguar scats were collected opportunistically during field work. We did not genetically confirm
396 that the scats were from jaguars but there are only two camera detections to date of another large felid
397 species (*Puma concolor*) in the study area compared to more than 1,600 jaguar detections (this study). We

were therefore confident that the vast majority (if not all) of the scats we collected were jaguar scats. Once collected, scat samples were stored in individually-labeled plastic bags and kept frozen until laboratory analysis. Undigested remains found in the scats were first isolated by rinsing the scats using a fine mesh, then dried and identified to the lowest taxon possible using a dissecting scope. We recorded jaguar diet using relative frequency of occurrence (number of occurrences of each prey item divided by the total number of scats). We compared our results to other published jaguar diet studies using either scat or kill site analysis with a sample size of at least 20. For comparative purposes, we grouped prey items into 'mammals', 'reptiles', 'fish' and 'birds' and standardized frequency of occurrence values to sum to 100%.

Social interactions among jaguars

We investigated shared space use among the resident jaguars collared in 2014-2015 (n=9), by quantifying the proportion of overlap at the 95% individual utilization distribution using the Autocorrelated Kernel Density Estimator (AKDE) in the R package 'CTMM' (Calabrese, Fleming, & Gurarie, 2016). Because jaguars exhibiting home-range overlap can still be avoiding each other temporally, we analyzed the frequency of social interactions by assessing simultaneous locations from both GPS data and camera data. GPS interaction rates were calculated using the package wildlifeDI (Long & Nelson, 2013) in R and defined as the number of times two GPS-collared jaguars were within 200 m of each other (Cavalcanti & Gese, 2009; Elbroch & Quigley, 2017). We defined camera interaction rates as the number of times two jaguars were observed together or within 30 min of each other. We collapsed interactions between individuals per day such that multiple contacts within the same day were not counted as new interactions for both the GPS and camera data.

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