



Collaborative behaviour and coalitions in male jaguars (*Panthera onca*)—evidence and comparison with other felids

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Abstract

Most large felids are classified as solitary species, with only lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) exhibiting social, collaborative behaviours. Herein, we present evidence of the formation of male coalitions by jaguars (*Panthera onca*), based on data from five studies conducted with camera trapping, GPS telemetry, and direct observations in the Venezuelan Llanos and Brazilian Pantanal. Out of 7062 male records obtained with camera traps or visual observations, we detected 105 cases of male-male interactions, of which we classified 18 as aggression, nine as tolerance, 70 as cooperation/coalition, and eight as unidentified. In two studies, two male jaguars formed stable coalitions lasting over 7 years each. In the Llanos, each coalition male paired and mated with several females. For male jaguar coalitions, we documented similar behaviours as recorded earlier in lions or cheetahs, which included patrolling and marking territory together, invading territories of other males, collaborative chasing and killing other jaguars, and sharing prey. However, different from lions or cheetahs, associated male jaguars spent less time together, did not cooperate with females, and did not hunt cooperatively together. Our analysis of literature suggested that male jaguar coalitions were more likely to form when females had small home range size, a proxy of females' concentration, while in lions, the male group size was directly correlated with the female group size. Similarly, locally concentrated access to females may drive formation of male coalitions in cheetahs. We conclude that high biomass and aggregation of prey are likely drivers of sociality in felids.

Significance statement

The division into social and solitary species in large felids has so far seemed unambiguous, with only lions and cheetahs classified as social species, in which male coalitions also occurred. Our data show that, under certain conditions, male coalitions may also form in jaguar populations. Factors that drive formation of male coalitions in lions and cheetahs, but not in other species of large cats, have not been clear until now. Our analyses indicate that in jaguars, lions, and cheetahs, the concentration of females likely plays the most important role. In jaguars, the probability of male coalition occurrence is highest in populations with the smallest mean female home range size (and thus likely high local density of females), while in lions, male group size is most strongly correlated with female group size.

Keywords Large felids · Carnivores · Cheetah · Group living · Lion · Reproductive behaviour

Introduction

Felids comprise a taxonomic group that is considered largely solitary (Sunquist and Sunquist 2002). The term “solitary” is generally understood as a social system in which females occupy exclusive home ranges that are usually overlapped by larger territories of males, intra-sexual relations are based on aggression, and there is no collaboration or participation

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of males in raising offspring (Caro 1989; Macdonald et al. 2010). Although some social interactions in solitary felids have been observed, they can instead be classified in the framework of social tolerance or spatial organization, and not as a true collaboration within a social group. Such behaviours include, for example, sharing large prey as observed in tigers (*Panthera tigris*, Schaller 1967), pumas (*Puma concolor*, Elbroch and Quigley 2017; Elbroch et al. 2017), and Eurasian lynx (*Lynx lynx*, Schmidt et al. 1997), or forming communal breeding colonies at sites with superabundant food resources to raise kittens, as observed in females of feral domestic cats (Macdonald et al. 2000; Bradshaw 2016).

Lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) are considered notable exceptions among wild cats, as for only these two species have the formation of social groups and cooperation within groups been documented (Packer 1986; Macdonald et al. 2010). In both species, males form groups known as male coalitions, while female social groups (“prides”) occur only in lions (Caro and Collins 1986; Packer et al. 1990; Caro 1994; Grinnell et al. 1995). Male coalitions occur not only in felids; such coalitions have been reported for various mammalian taxa and they are formed to expand and defend territory, and gain greater access to females or food resources, ultimately resulting in higher fitness through producing more offspring (Olson and Blumstein 2009).

In lions, males form groups of two to seven related or unrelated individuals that cooperatively fight with other males to take over and then defend pride females (Packer 1986; Packer et al. 1991). The males cooperate with each other and with females to defend territories, protect their offspring, hunt large-bodied prey, and defend kills from scavengers (Scheel and Packer 1991; Packer and Pusey 1997). Within the group, individual males typically have equivalent access to mate with females; males may copulate with the same females in sequence, resulting in group care of offspring and minimal female aggression to any coalition male (Packer and Pusey 1982, 1983; Chakrabarti and Jhala 2017, 2019). Infanticide by males against the offspring of prior males is a rule after invading a new territory and taking over a pride (Packer and Pusey 1983). Members of male lion coalitions gain higher fitness as they secure access to females, maintain the pride for longer periods, and produce more offspring than solitary males (Bygott et al. 1979; Packer et al. 1990, 1991). The evolution of male coalitions in lions was likely triggered by the aggregation of females in one pride, whereas high prey density was a necessary condition for the evolution of sociality among female lions (Packer et al. 1990). In particular, competition over high-quality territory with abundant prey has been proposed the most important driver of sociality in female lions (Mosser and Packer 2009). However, group sizes in male lion coalitions and female lion prides vary, with mean group size in males ranging from 1.0 (no coalitions) to 4.6, and in females from 1.3 to 9.2

individuals (Meena 2009; Celesia et al. 2010). Factors influencing this variation are unclear.

Male cheetahs may live alone or form a coalition of two or three, exceptionally up to five individuals which are usually, but not always, littermates (Caro 1990; Wachter et al. 2018; Broekhuis et al. 2019). Female cheetahs live alone or with their offspring and they use large, but highly overlapping home ranges, often aggregated in patches of good habitat (Caro 1994; Broomhall et al. 2003). Males do not maintain big territories encompassing several female territories as in other cat species. Some non-resident males (“floaters”) roam over large areas, in an attempt to gain access to females, while other residents maintain smaller, sparsely distributed territories in patches of good habitat where the chances of meeting and mating with females are high (Caro 1994; Marker et al. 2008; Melzheimer et al. 2018). Fights for a territory can be violent and bigger coalitions typically win over smaller groups (Caro and Collins 1987; Caro 1994). Female home ranges are usually bigger and encompass several smaller male territories (Caro 1994; Wachter et al. 2018). Females may copulate with different males of the same coalition, or with other males, such that multiple paternity is common (Gottelli et al. 2007; Mills et al. 2017). Male coalition partners are friendly to each other and spend most of the time together (Caro 1994). They may cooperate with each other and occasionally with females during hunting, but the males do not help rear offspring (Caro and Collins 1986; Caro 1994; Mills et al. 2017). Males are tolerant to cubs of other males and females do not need to defend the cubs from males (Caro 1994; Hunter and Skinner 2003).

Other large felids such as tigers (*P. tigris*), leopards (*P. pardus*), and jaguars (*P. onca*) are considered solitary (Packer 1986; Gittleman 1989). Macdonald et al. (2010) suggested that coalitions had not evolved in other *Panthera* species because of relatively low prey densities and closed habitat. Forested habitat with reduced visibility presumably does not offer competitive advantages for group hunting and instead favours ambush predation techniques (Sunquist and Sunquist 1989; Balme et al. 2012).

Jaguars are one of the closest evolutionary relatives of lions; the two species split about 1.5 million years ago. Jaguars and cheetahs are less closely related and share a common ancestor from nearly 11 million years ago (Johnson et al. 2006; Werdelin et al. 2010; Figueiró et al. 2017; Li et al. 2019). As revealed by paleontological analyses, the ancestors of modern jaguars, the European jaguar *P. onca gombaszoegensis*, first colonized the regions between northern Africa, central Europe, and western Asia; they then arrived in North and South America about 800,000 years ago (Kurtén and Anderson 1980; Marshall and Sempere 1991; Argant et al. 2007; Hemmer et al. 2010; Marciszak 2014). Currently, the jaguar ranges from northern Mexico through northern Argentina and is classified by the IUCN as Near

Threatened (Quigley et al. 2017). Although the jaguar is considered a solitary species (Rabinowitz and Nottingham 1986; Crawshaw and Quigley 1991; Azevedo and Murray 2007), some studies have suggested that male-male interactions can occur (Schaller and Crawshaw 1980; Cavalcanti and Gese 2009; Guilder et al. 2015; Kanda et al. 2019; Eriksson et al. 2021). However, unlike lions and cheetahs, jaguars usually live in more closed habitat, which makes direct behavioural observations difficult; thus, there is currently little information reported on jaguar social interactions.

Herein, we analysed male-male interactions and documented collaborative behaviours and male coalitions in jaguars. This information was collected from long-term camera trap surveys, telemetry, and observational studies conducted in two ecologically similar wetland ecosystems: the Llanos of Venezuela and the Brazilian Pantanal. In our analysis, we used male lion and cheetah coalitions as a reference point. In this context, we characterized male jaguar coalitions, their similarities, and differences with lion or cheetah coalitions. We hypothesized that male jaguars may form coalitions when females become more concentrated, similar to lions, but less so to cheetahs, for which the territorial system is different. We test this female concentration hypothesis by comparing our data with those from other intensively studied jaguar populations. Furthermore, we derive conclusions from comparisons with data gleaned from lion and cheetah literature to gain insights into the common factors that may drive the formation of male coalitions in large felids.

Study areas and methods

We analysed empirical data from five jaguar studies (Fig. 1) that included (1) long-term camera trap survey conducted in Hato Piñero, the Llanos, Cojedes, Venezuela (Jędrzejewski et al. 2014, 2017, 2021); (2) camera trap surveys, GPS telemetry, citizen science observations (with photographic/video records), and genetic analyses in Northern Pantanal I, Porto Jofre region, Fazendas São Bento and Jofre Velho, Mato Grosso and Mato Grosso do Sul, Brazil (Tortato and Izzo 2017; Devlin 2019; Hofman et al. 2019; Kantek et al. 2021); (3) camera trap survey and GPS telemetry in Northern Pantanal II, Taiamã Ecological Station, Brazil (Eriksson et al. 2021); (4) camera trap surveys, VHF and GPS telemetry, and direct observations in Southern Pantanal I, Fazenda San Francisco, Miranda region, Mato Grosso do Sul, Brazil (Azevedo and Murray 2007; Azevedo et al. 2010; Azevedo and Verdade 2012); and (5) camera trap surveys, GPS telemetry, and citizen science observations (with photographic/video records) in Southern Pantanal II, Caiman Ecological Refuge, Brazil (Morato et al. 2016, 2018; Kanda et al. 2019; Kantek et al. 2021; Thompson et al. 2021). In all these studies, individual jaguars were identified based on

the unique spot patterns. More information on study areas, methods, and collected material for each study is provided in Supplementary Information (Text S1 and Tables S1, S2).

The Llanos and Pantanal are ecologically similar wetland systems with pronounced wet and dry seasons, with the wet season characterized by significant flooding. Both wetlands are composed of a mosaic of natural savannah, marshes, patches of semi-deciduous dry forest and riparian forest, and cattle pastures (Zeilhofer and Schessl 1999; Silva et al. 2000; Polisar et al. 2003; Gonçalves et al. 2011). The Pantanal and Llanos have relatively high prey density and biomass and a similar composition of important prey species for jaguars, including capybara (*Hydrochoerus hydrochaeris*), caimans (*Caiman crocodilus* and *C. yacare*), peccaries (*Pecari tajacu* and *Tayassu pecari*), various species of turtles, and domestic livestock, mostly cattle (Schaller 1983; Hoogesteijn and Mondolfi 1996; Polisar et al. 2003; Azevedo and Murray 2007).

To determine how often contact between male jaguars may occur, we examined all recorded GPS/VHF simultaneous locations of any two males within 100-m distance (a distance we considered easy to sight another animal in largely open wetland habitat) and we classified them as close encounters with unknown type of interaction. Furthermore, we analysed all male-male interactions based on direct observations or records taken by the same camera trap within 10 min (assuming that individuals photographed at the same location within close temporal proximity are still within sighting distance or auditive communication) of any two male jaguars and classified them into the following categories: aggression, tolerance, cooperation/coalition, or unknown.

Aggression was identified by any signs of hostility, aggressiveness, fight, fear, or escape. Encounters were classified as tolerance when two males were recorded close to each other (e.g. feeding at the same prey carcasses) without any signs of aggression, but they were not classified as a collaboration/coalition. We classified two different male encounters as cooperation/coalition if they were (1) walking together or following each other, which we interpreted as patrolling territory together; (2) cooperatively chasing other jaguars; or (3) foraging together. We further analysed the data to detect additional behavioural features in detected male jaguar coalitions following the characteristics reported earlier for lion or cheetah coalitions, including (4) collaborative invasion of other male territories and (5) pairing or mating with a female in company of the associated male. To learn if male coalitions in jaguars may gain reproductive advantages, we examined numbers of unique females associated with each coalition male and other single males in each study area, based on camera traps or visual observations and recorded mating behaviour. However, statistical comparison of both groups was not possible because our

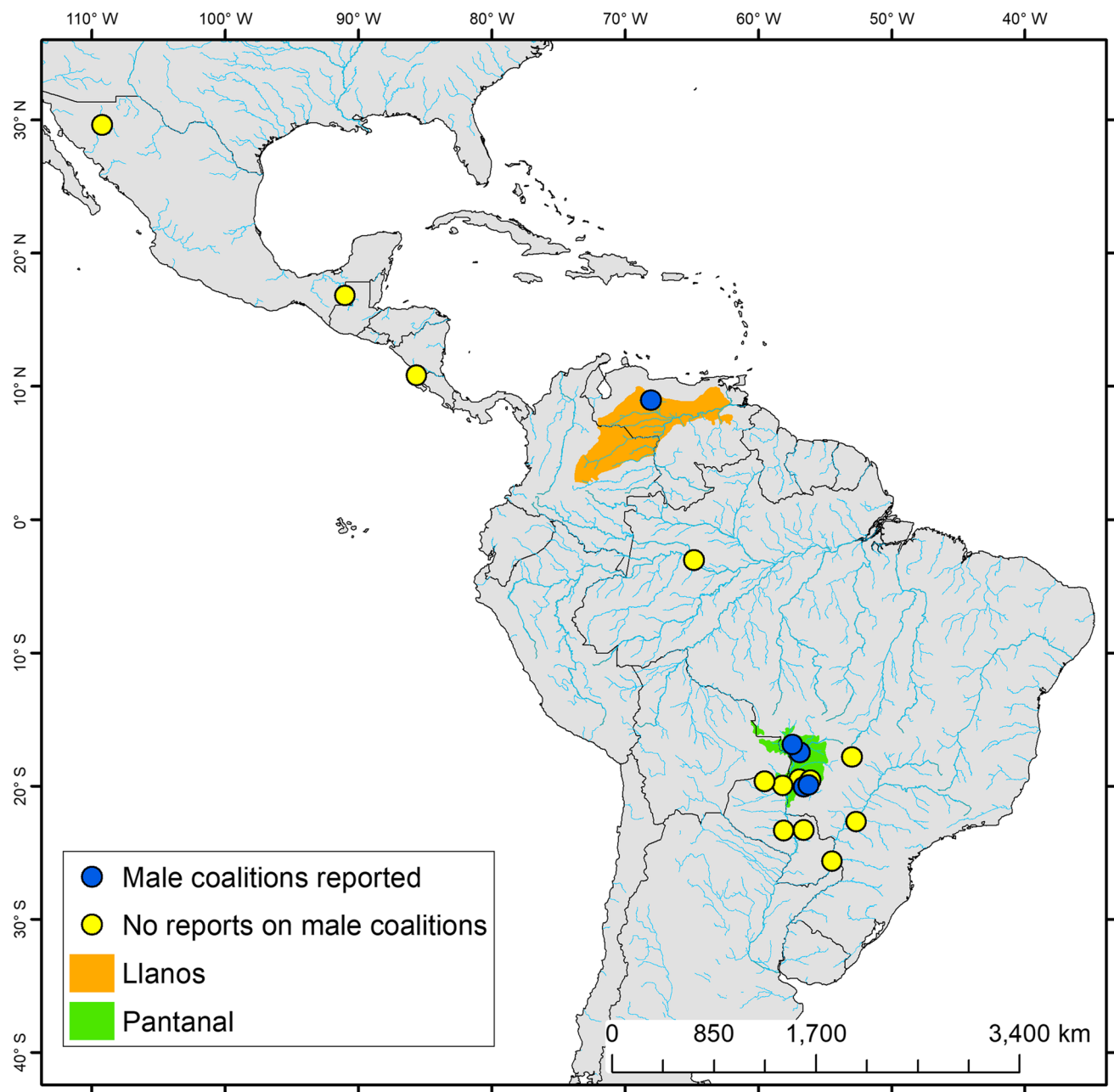


Fig. 1 Location of our five study areas where we recorded male jaguar coalitions and 13 other jaguar GPS telemetry studies (data published by Morato et al. 2018) with no reports on male coalitions. We

used data from all 18 studies in a logistic regression analysis to detect factors that may facilitate formation of male coalitions in jaguars

data were limited to the boundaries of our study areas and did not include all possible females with which the coalition or single males mated.

To directly test the female concentration hypothesis, we would need to compare female densities between our study areas and other studies where no coalitions were reported. However, numerous jaguar research projects that aimed at estimating population densities were typically limited to short periods of 3 months or less, often resulting in

relatively few jaguar records (Jędrzejewski et al. 2018), and thus were not capable of detecting male coalitions. In contrast, GPS telemetry studies typically aimed to estimate jaguar home range size and movement, and were usually conducted over longer periods and often occurred simultaneously alongside camera trap surveys. Such studies were more likely to detect male-male close encounters and interactions, including coalitions. To account for the varying consistency in available data, we combined our studies

with GPS telemetry data published by Morato et al. (2018) and calculated the mean female home range size (minimum convex polygon, 95% MCP) for each study area to derive an index of female concentration (Fig. 1, Table S5). We assumed that small home ranges were associated with higher female densities (based on jaguar data, Table S5, and regression between lion home range size and population density presented in Celesia et al. 2010). Three of our studies were already included in the GPS telemetry data set (Morato et al. 2018); for the remaining two studies (Los Llanos and Southern Pantanal I), we used estimates of female home range size from relevant earlier publications (95% MCP from Scognamiglio et al. 2003; 95% kernel density estimate from Azevedo and Murray 2007). To our knowledge, except for our five studies presented herein, no other research project has reported male coalitions.

We constructed a logistic regression using the observed presence/absence of coalitions at the 18 field sites and mean female home range size as an explanatory variable (data in Table S5). Based on the obtained logit values, we calculated probabilities of coalition occurrence for each study site (Hosmer et al. 2013) and plotted them against the mean female home range size. We also performed a similar logistic regression analysis with two other factors that potentially could influence grouping tendency in male jaguars—habitat productivity (approximated by the net primary productivity index NPP, Zhao et al. 2005) and forest cover—and we compared AUC values calculated for all three models (Hosmer et al. 2013). Habitat productivity is related to prey abundance (Field et al. 1995) and forest cover was suggested to play a role in the evolution of social systems in large felids because in forests, prey is more evenly distributed and there is no need to join up to defend patches with aggregated prey as it is in open savannahs with scarce waterholes (Mosser and Packer 2009; Macdonald et al. 2010).

To examine if similar factors determine coalition formation in both jaguars and in lions (both being more closely related and having more similar spatial organization system of male territories than in cheetahs), we analysed lion data provided in Meena (2009) and Celesia et al. (2010) (Table S6). We used female group size as an index for female concentration and calculated Pearson's correlations with male lion group size. For a comparison, we also correlated male lion group size with other factors that could potentially affect group size: lion population density, mean home range size (averaged for males and females, as provided by Celesia et al. 2010), prey biomass, rainfall, habitat productivity, and forest cover (Table S6).

All statistical analyses were performed with Systat 13 (Systat Software Inc., San Jose, CA, USA). It was not possible to record data blind because our study involved focal animals in the field.

Results

Male-male interactions and evidence for coalitions

Close encounters between male jaguars constituted 0.1% of all male locations obtained with GPS telemetry (33,611 total male locations) and 3.0% of records collected with camera traps or visual observations (total 7062 male jaguar records; Table 1). Aggressive interactions (18 cases) were recorded mostly in relation to mating (Southern Pantanal II) or territorial disputes (Los Llanos) and were less frequently observed at cattle carcasses. Tolerance (9 cases) was observed mostly at sites with high prey concentration (i.e. abundant fish in Northern Pantanal II) or at livestock carcasses, even in the presence of females (Southern Pantanal II). Out of a total of 105 interactions recorded by camera trapping or visual observations, we classified 70 as cooperation/coalition between two males (Fig. 2, Table 1).

In the Llanos, an association between two adult males was recorded from 2013 to 2018 (Figs. 2, 3, S1, S7, S8, Text S1, Tables S1, S2). Between 2013 and 2016 (see Text S1), the associated males were recorded together 40 times (9% of their total records, Table S2), walking together, marking territory, or when one was mating with a female (Figs. 2, 3). The annual home ranges of each male overlapped by 60%, 84%, and 74% in consecutive years (100% MCP home range estimates based on camera trap records; Fig. 3, Table S2). During that time, the two males gradually expanded their territory, invaded the territories of, and displaced at least six resident males (Fig. 3); the coalition males also secured access to the resident females (Text S1, Tables S3, S4, Figs. S7, S8). Over seven occasions, the associated males were recorded together in the presence of up to two resident females. The coalition ended when one of the associated males was likely displaced or killed by a new male, which also gained access to the resident females (Text S1).

In Northern Pantanal I, an association between two males was recorded between 2015 and 2018 (Text S1, Table S2). Over three occasions, both males were recorded together for prolonged periods, which included behaviours such as walking together, marking territory, sniffing the face of each other, and collaborative chasing of a young transient male (Figs. 2, S2). Additionally, they shared two cattle carcasses. The same males were previously recorded during camera trap and GPS telemetry studies (2011–2014) without any signs of association (Tables S1, S2). A genetic analysis revealed that the two males were not related (Kantek et al. 2021).

In Northern Pantanal II, two males were recorded together in 2015, over three separate occasions (29% of their total records), jointly searching for fish and walking

Table 1 Numbers of records of male-male encounters/interactions classified as aggression, tolerance, coalition, or unidentified. See Methods and Supplementary Information Text S1 and Tables S1, S2 for more details

Interactions/close encounters	Los Llanos	Northern Pantanal I	Northern Pantanal II	Southern Pantanal I	Southern Pantanal II	Total
Camera traps and visual observations						
Total number of male records	2668	NA	1609	210	2575	7062
Aggression	2 (0.1%)	NA	0	2 (1.9%)	14 (1.1%) 2 ^a , 12 ^b	18 (0.5%)
Tolerance	0 (0%)	NA	4 (0.5%)	0	5 (0.4%) 5 ^a , 4 ^b	9 (0.3%)
Coalition	40 (3.0%) 7 ^b	3	3 (0.4%)	22 (21.0%) 4 ^b	2 (0.2%)	70 (2.0%)
Unidentified	4 (0.3%)	NA	1	0	3 (0.2%)	8 (0.2%)
Total interactions	46 (3.4%)	3 (NA)	8 (1.0%)	24 (22.9%)	24 (1.9%)	105 (3.0%)
GPS telemetry						
Total number of male records	-	1652	24,813	-	7146	33,611
Close encounters with unknown type of interaction	-	0	14 (0.1%)	-	0	14 (0.1%)

^aRecords from livestock (mainly cattle) carcasses

^bRecords of male-male interactions that included presence of females (e.g. mating)

Percentages calculated on the combined records of both males involved in interactions over total male records (Table S2)

NA, data not available

together (Figs. 2, S3, Text S1, Table S2). Several other records of male-male interactions (Eriksson et al. 2021) included one pair that remained together and exhibited playful behaviour. However, we classified them as an unknown type of interaction (Table 1) due to undetermined relatedness and insufficient evidence of cooperation.

In Southern Pantanal I, two males formed a coalition between 2006 and 2014 (Figs. 2, S4, Text S1, Table S2). The males were recorded together a total of 22 times (31% of all their records); they patrolled territories together (11 times), rested side by side (7 times), communicated vocally with each other, mated with females in the presence of the other associated male (4 times), and shared an adult tapir (*Tapirus terrestris*) carcass. They were also reported feeding on the carcass of an adult female jaguar that they likely killed together (Azevedo et al. 2010). This coalition terminated when one male was wounded and then disappeared from the study area. The second male was evicted by an invading male almost 1 year later (Text S1).

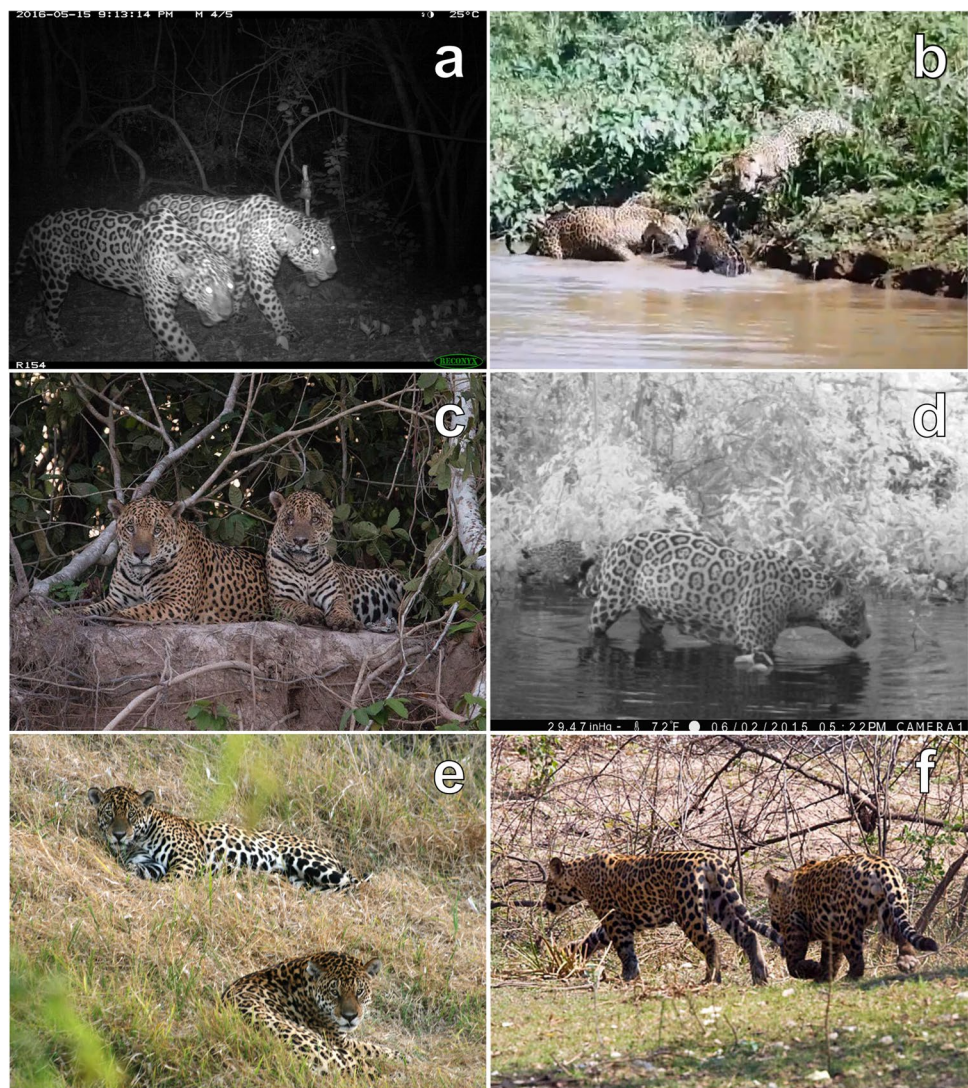
In Southern Pantanal II, we observed two different pairs of males; however, each one was observed only once, in 2010 and 2019 respectively (100% and 18% of their total records; Figs. 2, S5, S6, Text S1, Tables 1, S2). The first pair was observed resting and then walking away together. The second pair of males, new in the study area, displaced a resident male that exhibited aggressive behaviour towards them (Fig. S6).

Recorded behaviour of associated male jaguars in comparison to lion behaviour

We recorded several collaborative behaviours in associated male jaguars that have also been reported for lion or cheetah coalitions (Table 2). Similar behaviours included patrolling and marking territory together, chasing other males away together, invading territories of other males together, pairing or mating with females in the presence of an associated male, jointly searching for food, and feeding on the same prey item (Table 2, Text S1, Figs. 2, 3, S1–S6). Indirect evidence suggested that the males killed other jaguars together (Text S1). However, we have also recorded behaviours that are different from typical lion or cheetah behaviour, including frequent separation of the associated males from one another (Table S2) and more exclusive pairing with different females (Text S1, Table S3).

We also detected previously unknown specific behaviours related to interactions between associated males and females. In the Llanos, we recorded 11 cases where females, during the cub-rearing period, followed a coalition male that was likely not the father of the cubs, as we had previously recorded these females mating with the other coalition male (Fig. S7). This contrasted with the typical mating pair behaviour, where the male usually followed the female. Similarly, we recorded a female following both coalition males; this

Fig. 2 **a** Hato Piñero, the Llanos, Venezuela, May 2015: two male jaguars formed a coalition and cooperatively invaded territories of other males; a record of both males while expanding to the north-eastern part of the study area; **b** Fazendas São Bento and Jofre Velho, Northern Pantanal I, Brazil, September 2018: two associated male jaguars photographed chasing a transient subadult male (credit: Karen Souza); **c** Northern Pantanal I, Brazil, September 2015: two associated males resting together on the river bank (credit: Paul Donahue); **d** Taiaimã Ecological Station, Northern Pantanal II, Brazil, June 2015: two males searching for fish together; **e** Fazenda San Francisco, Southern Pantanal I, Brazil, September 2007: two associated males resting side by side (credit: Carolina Coelho); **f** Caiman Ecological Refuge, Southern Pantanal II, Brazil, 2010: two adult males walking together (credit: Larry Westbrook)



female was new in our study area; thus, her cubs were likely not sired by any of the coalition males (Fig. S8).

Although we did not record any female groups similar to prides of lionesses, we recorded three cases of two females close to the same male at the same time in the Llanos. We also recorded three other cases of two adult females staying close to each other (in the Llanos and Northern Pantanal II) or mutual tolerance between females visiting the same cattle carcasses (Southern Pantanal II; Table 1, Text S1).

Potential advantages from coalitions

In the Llanos, between 2013 and 2016, the two associated male jaguars coupled and mated with at least eight and six females each (Tables S3, S4, Fig. S7). For most other males, we recorded up to two females and only two solitary males were recorded with four and seven females each, respectively, although these numbers are certainly affected by

limited size of our study area (Tables S3, S4). In Southern Pantanal I, both coalition males were recorded with the same four females and one of them with an additional fifth female; however, only one of the males was actually recorded mating with the females (Table S4). Data for solitary males were not available for this area. In the Southern Pantanal II study, which was conducted in the largest area (more likely encompassing whole territories of some males) and over the longest timeframe (10 years), three solitary males were recorded to couple with as many as 13 females during the study (Table S4). As the coalition males only occasionally visited this study area (Table S2), their reproductive data were not available.

The recorded territorial tenure time of the coalition males was longer than that of solitary males (Text S1, Table S2). In the Llanos, each of the associated males was recorded in the study area for 6 and 7 years respectively, and they persisted in the region over a longer period than recorded

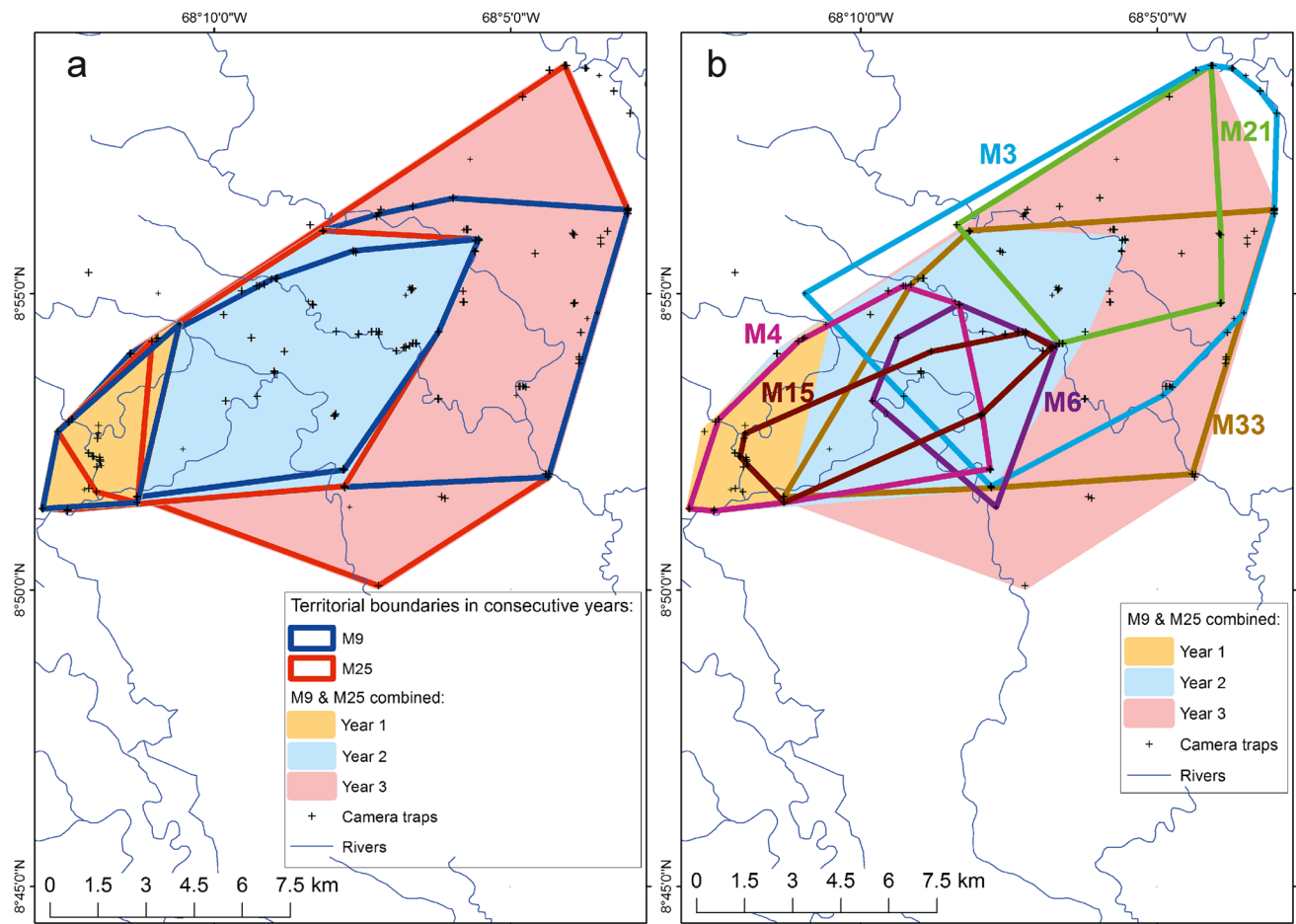


Fig. 3 Llanos, Venezuela; **a** the territorial expansion of the M9 and M25 male coalition during the first 3 years of the study (July 2013–August 2016), **b** the territorial boundaries (inside our study area) of the six solitary males that disappeared gradually following expansion

of M9-M25 coalition into their territories. The last record dates of these males were as follows: M15, 24 September 2013; M4, 5 August 2014; M6, 19 November 2014; M3, 4 August 2015; M21, 21 August 2015; M33, 15 December 2015. See Text S1 for more details

Table 2 Detection of behaviours exhibited by jaguars in each of the five study areas, grouped by behaviours typical for lion or cheetah male coalitions (1–5) and different from lions and cheetahs (6–7). Here, we annotate observations with direct evidence (DE; camera trap photos, telemetry records or observations documenting a given

behaviour), indirect evidence (IE; camera trap photos, observations, or other material, e.g. found carcasses, indicating high probability of a given behaviour), and no evidence (NE). For information on the evidence collected for each data entry, see Text S1, Tables S2–S4, and Figs. 1, S1–S9

ID	Behaviour	Los Llanos	Northern Pantanal I	Northern Pantanal II	Southern Pantanal I	Southern Pantanal II
1	Patrolling territory together	DE	DE	DE	DE	DE
2	Collaborative invading territories of other males	DE	NE	NE	NE	DE
3	Collaborative fights, chasing, or killing other jaguars	IE	DE	NE	IE	DE
4	Pairing or mating with a female in company of the other coalition male	DE	NE	NE	DE	NE
5	Joint search for food or feeding on the same prey	NE	DE	DE	DE	NE
6	Frequent separation from one another	DE	DE	DE	DE	DE
7	Coupling with different females by each male	DE	NE	NE	DE	NE

for any other solitary male, although our data did not allow for reliable estimates and comparisons of complete tenure times. In Southern Pantanal I, the two associated males lived in the study area for at least 6 and 7 years; however, data for solitary males were not available for that study.

The female concentration hypothesis: comparing potential drivers of male coalitions in jaguars and lions

Our data indicate that male associations in jaguars occur in areas characterized by small female home range size, which coincides with high jaguar population density and relatively high prey biomass (Table S5). The logistic regression based on data from 18 jaguar studies (Fig. 1, Table S5), five of which were our studies, revealed a significant relationship between the occurrence of male coalitions and female home range size (AUC = 0.954, sensitivity 0.80, specificity 0.92, Nagelkerke's $R^2 = 0.749$, $p < 0.001$), while there was no significant relationship with NPP (AUC = 0.554, sensitivity 0, specificity 1, Nagelkerke's $R^2 = 0.023$, $p = 0.59$) or forest cover (AUC = 0.531, sensitivity 0, specificity 1, Nagelkerke's $R^2 = 0.004$, $p = 0.82$; data in Table S5). Estimated probability of occurrence of male jaguar coalitions in intensively studied jaguar populations was high at small female home range sizes and dropped to 0 when female home range exceeded 100 km² (Fig. 4, Table S5).

Analysis of lion data (Table S6) revealed that mean male lion group size was most strongly correlated with female lion group size ($r = 0.54$, $N = 21$, $p = 0.01$, Fig. 5, Table 3) and was not significantly correlated with lion population density, prey biomass, mean home range size, NPP, rainfall, or forest cover ($r = -0.19$ to -0.08 , Table 3). Prey biomass in lion studies was on average eight times higher than in jaguar studies (Tables S5, S6).

Discussion

Based on data collected through a variety of research techniques, we documented, for the first time, a set of collaborative behaviours in jaguars that, until present, was reported only for lions and cheetahs, among large felids. Moreover, in two of our five studies, we found strong evidence for the formation of stable, long-lasting coalitions between two male jaguars, which possibly resulted in reproductive advantages. The recorded cooperative behaviours, similar to those found in lions and cheetahs, included joint patrolling and marking of territories, joint chasing and likely attempts of killing other males, invading territories of other males, mating with females in the presence of an associated male, and joint searching for food or feeding on the same prey (Packer 1986; Scheel and Packer 1991; Caro 1994). However, based on our

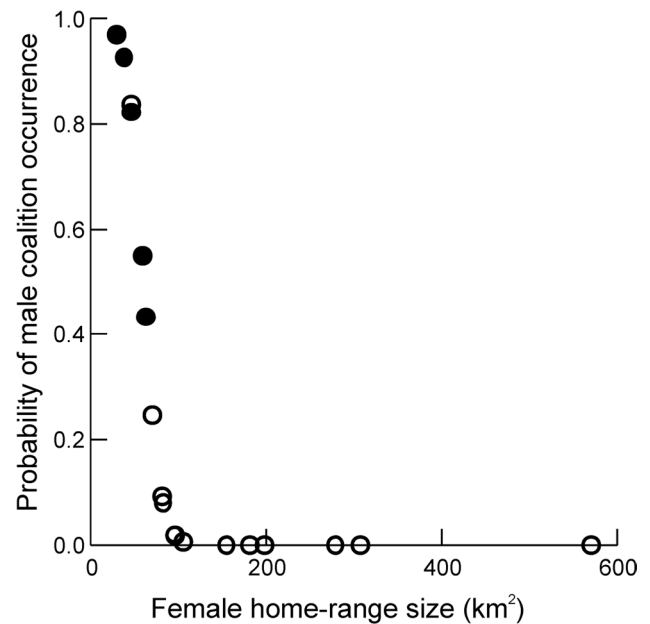


Fig. 4 Probability of male jaguar coalition occurrence predicted from the mean female home range size for 18 jaguar populations, based on the logistic regression. Black circles denote our five studies in which we found evidence for male associations; open circles, GPS telemetry studies (after Morato et al. 2018) for which no reports of male associations or collaborative behaviours were found. Home range size was approximated by 95% MCP (calculated for 16 studies included in Morato et al. 2018; taken from Scognamiglio et al. 2003 for the Llanos study) or 95% kernel density estimate (from Azevedo and Murray 2007 for the Southern Pantanal I study); see Methods and Table S5

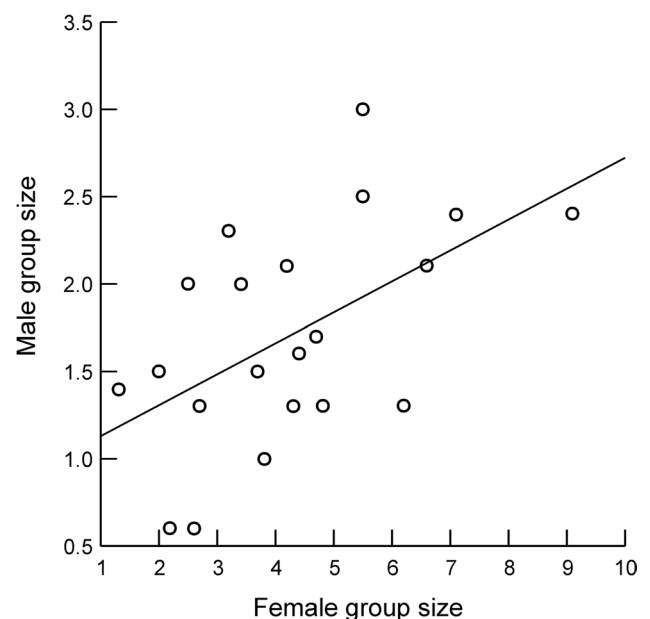


Fig. 5 Relationship between mean male lion group size and mean female lion group size. Data are provided in Table S6

Table 3 Pearson correlation coefficients between male lion group size and explanatory variables (data in Table S6)

	Male group size	<i>p</i>
Female group size	0.54	0.01
Lion population density	−0.09	0.70
Mean home range size	−0.10	0.70
Prey biomass	−0.19	0.42
Rainfall	−0.08	0.73
NPP	−0.09	0.69
Forest cover (%)	−0.09	0.70

and other studies, there remain several general characteristics that distinguish male jaguar coalitions from those found in lions or cheetahs, such as average group size (at most two males form a coalition in jaguars, while in lions and cheetahs more males can group together), spatial organization and mating system (e.g. no female groups in jaguars in contrast to lions, male jaguar territories are larger than female territories in contrast to cheetahs), and lack of cooperative hunting or visible cooperation with females (the latter typical for lions only). In our analysis, we also found more specific behavioural differences in male coalition jaguars versus lions and cheetahs, including spending more time separated, and likely more exclusive relationships with females.

We also detected a previously unknown behaviour in females wherein they followed one or both associated males, which likely had not sired cubs of those females. Likely, this escorting behaviour was associated with mitigating the risk of infanticide. The escorting and paternity confusion behaviours exhibited by female jaguars to protect their cubs and prevent infanticide by adult males were documented in other studies in the Pantanal and Llanos (Stasiukynas et al. 2021). Infanticide by jaguar males was recorded in one of our study sites, although not by coalition males (Tortato et al. 2017). Interestingly, infanticide does not occur in cheetahs (Caro 1994), which makes them different from jaguars and lions.

Our analysis of data previously published on jaguars and lions supported our hypothesis, wherein a key driver of the formation of male coalitions in both species is the concentration of females. In lions, females live in prides, which favours the formation of male coalitions because joining together facilitates acquiring access to females and provides reproductive benefits to all members of the coalition (Bygott et al. 1979; Packer and Pusey 1982, 1997; Packer et al. 1990). In jaguars living with favourable prey conditions, female home ranges can be small and partially overlapping, resulting in locally higher concentration of females (Azevedo and Murray 2007; Table S2, this study), which may promote associations between males to gain access to more females, similar to lions. However, female jaguars do not group, and they maintain only partially overlapping

territories; this may force the associated males to temporarily split when visiting females and consequently may contribute to less time spent together. This is also a likely reason why this strategy is relatively rare and possibly less advantageous for jaguars; when apart, a male can be attacked more easily by another male. In our studies, only a small fraction of males formed coalitions, and we found evidence that such coalitions could be terminated by a fight between one of the coalition members with other, solitary males.

In cheetahs, male coalitions do not defend exclusive access to territories of several concentrated females as lions and jaguars do, but instead they defend areas where their chances of mating with several females, whose large territories are greatly overlapping, are highest. Joining together increases the chances to take over a better territory and mate with a higher number of females. However, females may mate with various resident and non-resident males, which results in frequent litters with multiple paternity (Gottelli et al. 2007; Mills et al. 2017). Consequently, males might not know which offspring is theirs and infanticide in cheetahs does not occur (Caro 1994). Thus, in all three species, spatially concentrated access to females is likely the main driver of forming male coalitions. However, as revealed by our study, the territorial expansion and likely attempts at monopolizing females by male jaguar coalitions seem to fit better with the lion system than with the cheetah system (Caro 1994; Packer and Pusey 1997).

Jaguars are currently classified as a solitary species, like tigers and leopards (Sunquist 1981; Gittleman 1989; Seymour 1989; Bailey 1993; Sunquist and Sunquist 2002; Macdonald et al. 2010). However, frequent male-male contacts, mutual tolerance, and a high degree of home range overlap between male jaguars (higher than in other solitary *Panthera* species) were also documented in earlier studies (Schaller and Crawshaw 1980; Cavalcanti and Gese 2009; Guilder et al. 2015; Eriksson et al. 2021). Together with our studies, this indicates that jaguars may have an intrinsic predisposition for collaborative behaviours and forming male coalitions that may appear under favourable conditions (e.g. high prey density). Both the Llanos and the Pantanal sites, where we detected male jaguar coalitions, are characterized by fairly high prey biomass (Schaller 1983; Polisar et al. 2003; Table S5, this study). However, prey biomass in lion studies was estimated at significantly higher levels than anywhere in jaguar range and was on average eight times higher than at our study sites. Lower prey biomass is likely another important factor limiting female densities and the frequency of male coalitions in contemporary jaguar populations. For the most of their evolutionary history (until 15,000–10,000 years before present), jaguars coexisted with rich communities of Quaternary megafauna, resembling conditions that lions still encounter today in Africa (Kurtén and Anderson 1980; Martin and Klein 1989; Marshall and

Sempere 1991; Arroyo-Cabrales 2002; Fariña et al. 2013). The presence of cattle increases total prey biomass in present-day jaguar habitat and may be another important factor facilitating the formation of coalitions. In the studies presented herein, we recorded collaborative behaviours where wild prey was abundant (all our study sites) and cattle were present (four out of five sites). Moreover, male-male tolerance in our studies was mostly recorded at cattle carcasses. However, contrary to our expectations, we did not find any evidence that prey biomass or habitat productivity was significantly related to coalition formation in jaguars or lions, although both factors have strong impacts on population density and home range size in large carnivores (Karanth et al. 2004; Jędrzejewski et al. 2018; Thompson et al. 2021), suggesting some more complex explanation. A candidate factor, together with prey biomass, is possibly prey aggregation (Mosser and Packer 2009; Macdonald et al. 2010). Higher concentrations of prey near water bodies occur both in the African savannahs and in the Llanos and Pantanal wetlands, in the latter two, enhanced by the presence of cattle herds (Polisar et al. 2003; Devlin 2019; Eriksson et al. 2021). This factor may significantly contribute to the concentration of females and the formation of male coalitions in all three species: lions, cheetahs, and jaguars (Caro 1994; Mosser and Packer 2009). However, our analysis did not support predictions that grouping tendency would be higher in more open habitat (Macdonald et al. 2010), suggesting that forest cover may not be a good predictor of prey aggregations.

In contrast to lions and cheetahs, which benefit from grouping by increasing their hunting success (Packer et al. 1990; Caro 1994), in our jaguar studies, we did not observe cooperative hunts and rarely recorded joint searching for food or sharing the same prey item between the associated males. Although cooperative hunting in jaguars may still be documented in future studies (e.g. with the development of modern non-invasive remote observation techniques), our results indicate that the main goal of male jaguar associations is to potentially gain reproductive advantages by invading other male territories and securing access to females. However, we could not document all females that each male mated with because our records were spatially limited to camera trap stations or visual observations. Additionally, our study areas were small compared to the territory size of male jaguars, and we likely missed several females that mated with monitored males outside our study sites.

Collaborative behaviours were likely not recorded earlier in jaguars due to the methodological limitations of prior studies (e.g. short duration of most of camera trapping projects; Jędrzejewski et al. 2018). Although, prior research (e.g. Cavalcanti and Gese 2009) and this study show that most male jaguars are solitary, and collaborative or tolerant behaviours are relatively rare in jaguar populations, yet they can and do occur. More studies with adequate field

methodology are needed to investigate how often and under which conditions these behaviours may occur throughout the jaguar's range. Our analysis of GPS telemetry data suggests that collaborative behaviours are more likely in habitat where female home ranges are small, and densities are high. Nevertheless, some close contacts between male jaguars may also occur in less productive parts of jaguar range. For example, in the dry Chaco of Paraguay, genetic analyses revealed that jaguar scats deposited regularly at the same sites during the same nights belonged to two unrelated jaguar males (Giordano 2015).

Our findings highlight the importance of a multi-method, long-term approach when designing studies on social interactions or behaviour of elusive species that are difficult to observe, such as jaguars and several other felids. Combining data from camera trap surveys, direct observations, GPS telemetry, and genetic analyses conducted over several years resulted in discovery of collaborative behaviours between male jaguars in our studies. A similarly designed study by Elbroch et al. (2017) documented frequent visits and sharing of prey between neighbouring pumas in the Yellowstone National Park region. Future studies with a similar approach may reveal more cryptic behaviours and enable better understanding of the evolution of the social life of large felids.

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Author contribution RH and WJ gave the initial idea and coordinated collaboration on this paper; WJ, HVBC, FA, RH, ALD, FT, CEE, CEF,

MA, RC, and GG provided jaguar data; WJ, KS, ALD, MA, RGM, RH, FT, HVBC, and AJG collected jaguar and lion literature data; GV performed GIS analysis and prepared NPP and forest cover variables; WJ performed the statistical analysis and wrote the first draft of the manuscript. All authors commented on the subsequent drafts, worked on the final version of the manuscript, and approved it.

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Data availability All data used in this study are included in the Supplementary Information.

Declarations

Ethics approval All studies were conducted in accordance with the international, national, and/or institutional guidelines and regulations for the animal research. Each study had the appropriate permits. For the Llanos study, the permission was granted by Oficina Nacional de Diversidad Biológica, with licence ID: Oficio 0103/Providencia 000103 and Oficio No 1591/Providencia n 0055. Northern Pantanal I was conducted under the Licence SISBIO/ICMBio 43980. Northern Pantanal II study was approved by Instituto Chico Mendes de Conservação da Biodiversidade with permit SISBIO 30896–3. For the Southern Pantanal I, the permission was granted by IBAMA, with the license number 02027.007013/03–81. Southern Pantanal II study was approved by National Research Center for Carnivores Conservation—ICMBio/CENAP with the license numbers no. SISBIO 30.053, 52.734, and 61.844.

Competing interests The authors declare no competing interests.

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