



**Programa de Pós-graduação em Ecologia e Conservação**

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**Long-term population dynamics of jaguars (*Panthera onca*) and the importance of refuge during extreme fire events.**

Abigail Allen Martin



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Supervisor: Luiz Gustavo Rodrigues Oliveira Santos

Co-Supervisor: Fernando Rodrigo Tortato

## **Evaluator committee**

**Dr. Ronaldo Morato ([rmorato@panthera.org](mailto:rmorato@panthera.org))**

**Dr. Valeria Boron ([valeria.boron@gmail.com](mailto:valeria.boron@gmail.com))**

**Dr. Flávia Tirelli ([flavia.tirelli@gmail.com](mailto:flavia.tirelli@gmail.com) )**

**Dr. Caroline Leuchtenberger ([caroleucht@gmail.com](mailto:caroleucht@gmail.com))**

**Dr. Marcus Vinicius Vieira ([mvvieira@gmail.com](mailto:mvvieira@gmail.com))**

I would like to dedicate this work to the late *Peter Crawshaw Jr.* Your inspiration, friendship and kindness reminds me always of why I chose this path.

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## **Abstract:**

Understanding the impact of extreme environmental events on apex predators is critical for conservation planning in a changing world. This study examines the long-term population dynamics of jaguars (*Panthera onca*) in the northern Pantanal, Brazil, with a focus on the ecological role of riverine forest as refuge. Over 11 years, we conducted systematic mark-recapture surveys, recording 4,161 jaguar sightings and analyzing population parameters including survival, recruitment and population growth on all demographic groups (sex and age). Our findings reveal that riverine forest mitigates the demographic impact of wildfire by providing refuge habitat for displaced individuals and supporting local populations during disturbances. While survival rates declined (0.92 – 0.79) from before to during (0.81 – 0.60) and further after the fires (0.79 – 0.5), recruitment surged (0.2 to 0.61) as individuals sought refuge and then dropped post-fire (0.61 to 0.25). Notably cub recruitment increased post-fire, underscoring the importance of habitat quality in reproductive success. These dynamics highlight the dual role of refuges in buffering immediate impacts and facilitating long-term population recovery. Our study is the first of its kind to dive deep into jaguar population demographics covering both males and females and adults and cubs. This research underscores the necessity of preserving riverine systems as ecological refuges and enforcing conservation policies to mitigate the impacts of both climate and human induced disturbances.

## **Resumo:**

Compreender o impacto de eventos ambientais extremos sobre predadores de topo é fundamental para o planejamento da conservação em um clima em mudança. Este estudo examina a dinâmica populacional de longo prazo das onças-pintadas (*Panthera onca*) no norte do Pantanal, Brasil, com foco no papel ecológico das florestas ripárias. Ao longo de 11 anos, realizamos levantamentos sistemáticos de marcação-recaptura, registrando 4.161 avistamentos de onças-pintadas e analisando parâmetros populacionais, incluindo sobrevivência, recrutamento e crescimento populacional em todos os grupos demográficos (sexo e idade). Nossos resultados revelam que as florestas ripárias mitigam o impacto demográfico dos incêndios florestais ao oferecerem habitat de refúgio para indivíduos deslocados e ao apoiar populações locais durante distúrbios. Embora as taxas de sobrevivência tenham diminuído durante e após os incêndios, o recrutamento aumentou à medida que os indivíduos buscaram refúgio. Notavelmente, o recrutamento de filhotes aumentou após os incêndios, destacando a importância da qualidade do habitat para o sucesso reprodutivo. Essas dinâmicas ressaltam o papel duplo dos refúgios em amortecer impactos imediatos e facilitar a recuperação populacional a longo prazo. Esta pesquisa destaca a necessidade de preservar os sistemas ripários como refúgios ecológicos e de implementar políticas de conservação para mitigar os impactos de distúrbios induzidos pelas mudanças climáticas.

**Keywords:** Wildfire, climate change, Demographic parameters, survival, recruitment Large carnivore ecology

## **Introduction:**

Major threats to biodiversity, such as climate change, pollution, habitat loss, invasive species and wildfires are increasingly jeopardizing the stability of ecosystems worldwide (Wudu et al., 2023). These factors, often referred to as the "evil five" biodiversity threats, interact in complex ways, leading to nonlinear responses in biodiversity and ecosystem stability. Among these, climate change stands out as the most pervasive, significantly impacting biodiversity, and ecosystem functions and services (Capon et al., 2013; Estes et al., 2011). Climate change is recognized as a primary driver of species extinctions (Borges and Loyola, 2020; Capon et al., 2013), creating a feedback loop that exacerbates other threats. Specifically, climate change induces conditions creating more severe drought, reducing rainfall and creating more prone conditions for wildfires to ignite and spread. These fires, in turn, further increase climate change effects by releasing large amounts of carbon dioxide, continuing a cycle of environmental degradation (Wantzen et al., 2024). When wildfires occur alongside climate change, the combined impact is even more detrimental, leading to more frequent and intense fires that pose a severe threat to biodiversity and the resilience of ecosystems.

It is well known that many plant and animal populations have evolved with fire disturbance and even benefit from it at certain life stages (Liedloff et al., 2018). However, most extreme wildfires pose significant challenges, direct mortality from heat and smoke inhalation, habitat loss and the need for species to recolonize (Liedloff et al., 2018). Fires also impact on food quality, distribution, and shelter availability, increasing predation vulnerability and making fauna more susceptible than flora (Liedloff et al., 2018; Watson, 2002). Even animal species that

evolved in fire-prone ecosystems rely on such as moving away from fire or seeking shelter in burrows and dens (Selwood et al., 2019), moving towards large water sources (Reside et al., 2019) or some type of ecological refuge (Pausas, 2019).

Refuges are critical in conservation, defined as places where organisms can survive through unfavorable conditions (Keppel et al., 2012). The identification and protection of refuges are becoming central to conservation efforts, with refuges expected to be key mechanisms for species survival in the future (Berryman et al., 2006; Borges and Loyola, 2020; Reside et al., 2019; Robinson et al., 2013). These can include rocky environments, montane areas, riparian zones, and wetlands, identified as vital for protecting biodiversity against rapid environmental changes (Selwood and Zimmer, 2020). Riverine areas, in particular, are considered hotspots for adaptation to climate change (Capon et al., 2013). These areas support high adaptive capacity due to their environmental variability and connectivity, allowing species to move and adapt to changing conditions. The connectivity within and between riverine ecosystems provides essential movement pathways, making these areas crucial refuges, especially during extreme fire events.

Most large predators including the big cats (genera *Panthera*) are threatened with extinction, presenting continuous worldwide population declines and range contractions despite targeted conservation research and actions (Estes et al., 2011; Kantek et al., 2021). Large cats are long lived species (i.e. 12-15 years) that usually present low population densities, composed by individuals with slow reproduction rates that demand vast conserved areas to set their home ranges, and healthy populations of prey to sustain their energetic requirements (Carbone et al., 2011; Crooks et al., 2011). Although habitat loss and killing due to retaliation or fear are considered the major threats to big cat conservation, current climate events such as extreme droughts and wildfires have been flagged as important conservation issues (Bardales et al., 2024;

Bogoni et al., 2023; De Barros et al., 2022; Menezes et al., 2021).

That is the case of jaguars (*Panthera onca*) as well, the largest cat in the Americas and top predators of the neotropics (Hunter, 2015; Morato et al., 2024). (Hunter, 2015; Morato et al., 2024). Considered Near Threatened with decreasing population trend by the IUCN (IUCN, 2016). They have lost over half of their historical range due to land use transformations, and the habitat that currently remains today is continually lost to deforestation and wildfires (Bogoni et al., 2023; De Barros et al., 2022; De La Torre et al., 2018; Kantek et al., 2021). Although a growing amount of current jaguar range is composed of small populations (Paviolo et al. 2016), large extensions of conserved habitat hold connected populations through the Pantanal wetland and western Amazonia. However, both locations are suffering high deforestation rates and increased frequency of extreme droughts and wildfires (Berlinck et al., 2022). This has called attention of media and conservationists about the impact of these events (Tomas et al., 2021), specially on jaguars (Bardales et al., 2024; Jędrzejewski et al., 2018; Menezes et al., 2021). Due to wildfires and deforestation that occurred in the Amazon from 2016 to 2019 an estimated number of 1,470 jaguars were displaced or killed (Menezes et al., 2021). In 2020, an estimated 1668 individual jaguars were impacted by the wildfires in the Pantanal (De Barros et al., 2022). These emerging threats, added to the previous ones, put jaguars at an even higher risk of extinction and it is important to understand how these new threats affect their populations. Jaguars are among the most aquatic of the world's big cats, feeding on aquatic and semi-aquatic prey (i.e., caiman and capybara), selecting major riverine forests to set their home range, move and disperse through the landscape (Eriksson et al., 2022; Quigley and Crawshaw, 1992). Beyond being the preferential habitat, riverine forests can act as refuges, buffering the impact from extreme drought and large wildfires, potentially saving resident individuals and providing a

temporary area for survival of individuals from a far. Riverine areas tend to be naturally wetter than the surrounding landscape. As a result, they are less affected by fire and support faster vegetation recovery afterward. Consequently, these areas can serve as a refuge for prey species, attracting terrestrial herbivores and sustaining aquatic and semi-aquatic species that remain available for predators immediately after the fire. Robinson et al. (2013) stated that refuges have three main functions in relation to wildfires: (1) they enhance immediate survival during a fire event, (2) facilitate the persistence of individuals and populations after fire and (3) assist in the re-establishment of populations in the longer term.

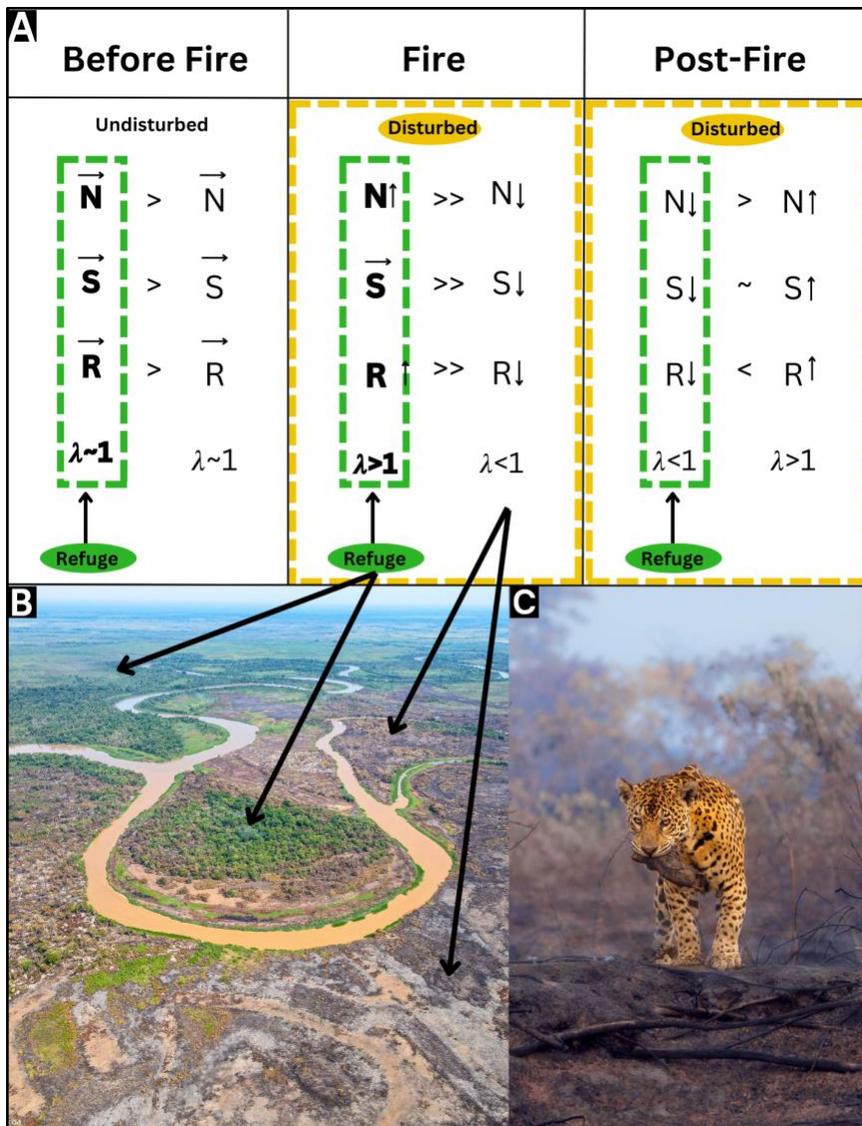
As set by Robinson et al. (2013), the understanding of population dynamics and associated demographic parameters (survival and recruitment) are key information to support adequate conservation and management strategies in the context of wildfires (Athreya et al., 2013). Currently, we have observed an increase in population studies of wild cats triggered by the popularization of camera traps in ecological studies across the globe (Jędrzejewski et al., 2018; Rocha et al., 2016). However, most studies are site-specific, lasting only 3-5 years, where researchers typically access abundance in one point at space and time (Karanth et al., 2004). Therefore, we still lack detailed long-term information about big cat population dynamics (i.e., survival, recruitment, population growth, turnover) to allow us to plan and implement specific management actions. Assessing population parameters demands long-term population studies, and becomes especially important when we aim to understand the effect of seasonal or multiannual extreme events on big cat populations.

Here we expanded (Robinson et al., 2013) ideas and proposed a more detailed demographic expectation for an area to be robustly recognized as a refuge. We hypothesize that refuges must provide a demographic buffer for the population, affecting its parameters:

abundance (N), apparent survival (S), recruitment (R) and population growth ( $\lambda$ ). Before fire (Figure 1A; left panel), in the undisturbed environment, these parameters will be stable but greater inside the refuge than outside. During the fire N, S, R and  $\lambda$  will be much higher inside the refuge than in the disturbed surrounding. Although S stable, N will increase mainly due to the increases of R related to the influx of displaced individuals coming from disturbed areas, which in turn will yield a  $\lambda$  higher than 1 (i.e.; population growth, Figure 1A; center panel). Post-fire we would expect N to decrease inside the refuge but still remain greater than the disturbed environment, S should decrease due to the refuge density-dependence competition, which will induce dispersal from refuge to recovering disturbed areas; as observed for S, R also will decrease, but due to lack of dispersal individuals coming from recovering surrounding areas, resulting in a  $\lambda < 1$  (population decline, Figure 1A; right panel). On the other hand, the population  $\lambda$  outside the refuge, currently recovering from disturb, will be higher than 1 (repopulation) due the increase in S (recovery of suitable habitat), and a steep increase in R related to the influx of the individuals surplus yield by the refuge. Note that refuge plays a fundamental role by receiving displaced individuals from disturbed areas, keeping local survival and reproduction, and yielding temporary individual excess that can disperse and further repopulate once disturbed areas are in recovery process. It is important to mention that heightened abundances within the refuge can lead to increased competition for limited resources (Hassell, 1998; Loery and Nichols, 1985), elevated risk of disease transmission (Maji et al., 2020), and higher predation pressures (Knowlton, n.d.; Pan et al., 2024), potentially impacting long-term population persistence. These density-dependent effects highlight the complex dynamics within refuge during and after extreme disturbances.

For this study, we focused on the jaguar and described the long-term population dynamics (11 years) seen along the river margins, which was considered a potential ecological refuge. During the course of our study, catastrophic wildfires burned almost 30% of the Brazilian Pantanal in 2020, providing an opportunity to test if riverine habitat plays the role of an ecological refuge, and if it is, how a long-lived top predator population responds to wildfire inside the refuge. We also tested for differences in demographic parameters among ages, genders, then assessed the effect of rainfall and extreme wildfire events on these parameters. Specifically, by controlling for imperfect detection, we estimated abundance, apparent survival, recruitment and population growth before during and after the 2020 fire event. Then, we tested the effect of sex (male and female), age (cub and adult), annual rainfall, and wildfire (before, during and after) on the survival and recruitment parameters. We hypothesize that cubs will have lower survival and recruitment than adults due to their vulnerability to environmental pressures, predation and dependence on maternal care. Cubs are less experienced and more susceptible to disturbances, making their survival and successful recruitment into the population more challenging (Fragoso et al., 2023). Additionally, we hypothesized that females would have higher survival and lower recruitment than males. Females tend to have a more stable home range which can enhance their survival rates (Bisht et al., 2019; Lebreton et al., 1992). However, males often engage in territorial disputes and exhibit higher dispersal tendencies, potentially increasing their recruitment but also exposing them to greater risk that may lower their survival (Funston et al., 2003). Because we believe that riverine forests act as a buffer during years with extreme wildfires, we also expected that there would be a decrease in survival rates during and right after the fire, but we would observe an increase in recruitment of adults coming from adjacent areas (Meddens et al., 2018; Morelli et al., 2016; Watchorn et al., 2024). This increased

recruitment should (over) compensate for the local drop in survival and, in turn, keep local population growth still positive or *in equilibrium* ( $\lambda = 0$ ). We also tested if there is an effect of rainfall on these parameters, since jaguars are a species closely linked to water (Eriksson et al., 2022; Quigley and Crawshaw, 1992).



**Figure 1:** A) Schematic diagram showing hypothetical population changes expected to occur before, during and after a fire disturbance event. We are investigating four different parameters: (N) abundance, (S) apparent survival, (R) recruitment ( $\lambda$ ) and population growth. Before fire we assumed the surrounding environment and refuge (green dashed rectangle) is undisturbed. During fire the surrounding environment is

disturbed (yellow dashed square) but the refuge remains undisturbed. Post-fire the surrounding environment is disturbed but in recovery. B) Actual images of what we are considering a refuge and a disturbed environment.. C) Focal species jaguar (*Panthera onca*) in the fire torn environment, credit: D. Paiva.

## 1. Methods

### 2.1 Pantanal Study Region

The Pantanal is the largest contiguous freshwater wetland globally, about 166 thousand km<sup>2</sup>. One of the most outstanding characteristics is its annual cycle, flood and drought. Since the great floods of the 1970s, this larger cycle has become unbalanced, perhaps as a consequence of anthropogenic changes outside of the Upper Paraguay River basin (Berlinck et al. 2021, Garcia et al. 2021, Tomas et al. 2021, Libonati et al. 2020). Since 2019, the Pantanal has suffered a prolonged drought that has spelled disaster for the region, and subsequent fires have engulfed hundreds of thousands of hectares (Garcia et al 2021). For instance, northern Pantanal has currently experienced lower levels of soil moisture, 13% more days without rain than in the 60's, and the water mass is 16% less during the dry season in the last 10 years (Krueger et al., 2022; Marengo et al., 2016b, 2016a). Between 2004 and 2022, 10% of all protected areas in the Pantanal had a fire return interval of 2 years or less (Moreira et al., 2024). In 2020, an estimated 47 thousand small to medium sized mammals died from megafires, sampled from SESC (Social Service of Commerce) a Pantanal Private Natural Reserve, located in the Northern Pantanal probably due to lack of refuges and limited escape opportunities (Brack et al., 2024).

The Pantanal is categorized as fire-dependent and the presence of fire has dated back far before oldest human settlements (Power et al., 2016), however the Pantanal has a very peculiar dynamic with its seasonal flooding and fires which shaped its biota and plant communities.

Natural fires caused by lightning in the peak dry season promote germination of some plants and with dynamics of yearly flooding it creates monodominant vegetation types (Pivello et al., 2021; Pott and Pott, 2004). Though this biome is categorized as fire-dependent because of its vast mosaic of grasslands and savannas, the riverine forest along its major water bodies are considered fire-sensitive. These intense and reoccurring fires can gradually reduce the extension and resilience of these forests (Hébert-Dufresne et al., 2018).

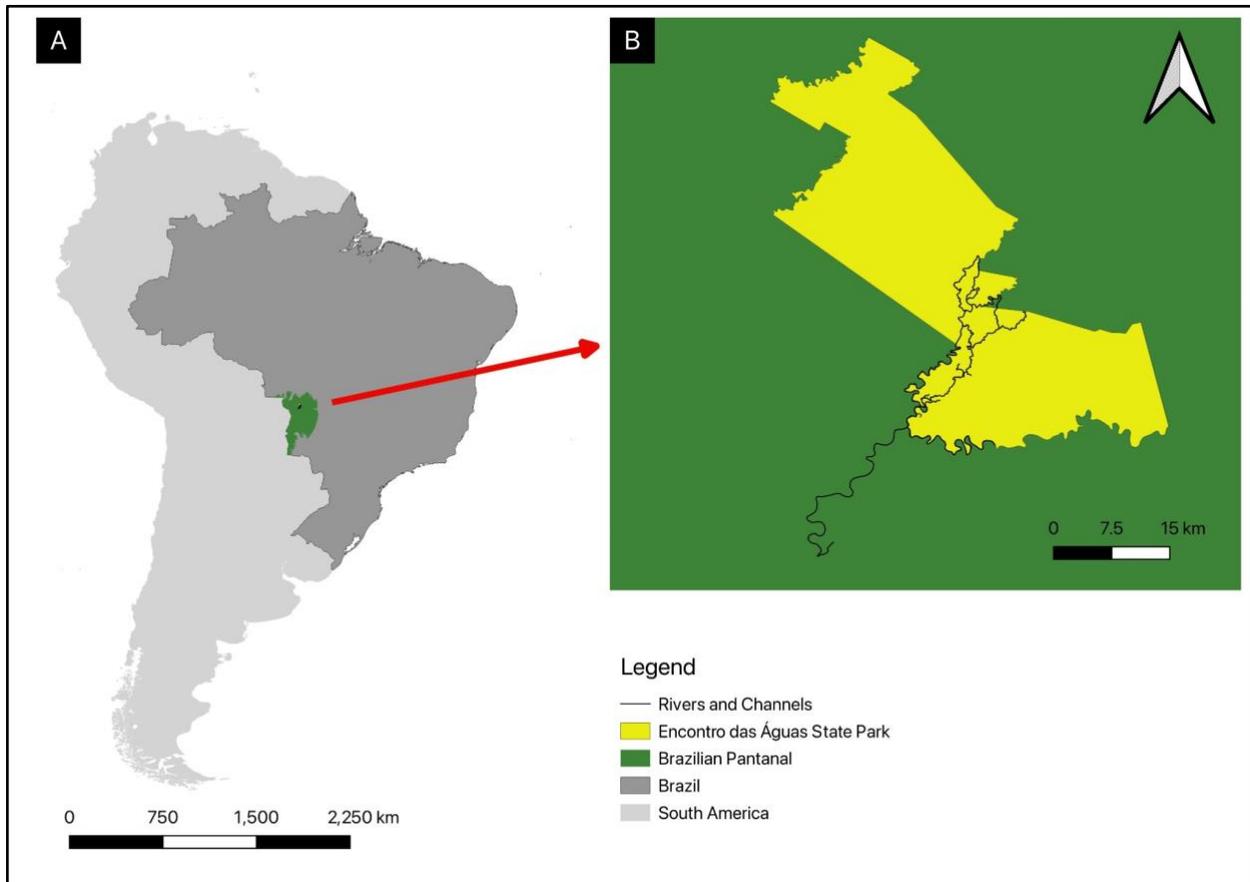
The study area is situated within one of the 51 Jaguar Conservation Unit (JCU), recognized as a critical habitat for the southwestern jaguar population in South America (Sanderson et al., 2002). JCUs are areas of importance for jaguar conservation, defined as areas able to maintain a viable jaguar population (at least 50 adult individuals) and promote their long-term survival. These areas are selected based on the presence of adequate prey resources, habitat connectivity, and minimal human disturbances (Sanderson et al., 2002; González-Gallina et al., 2022).

## *2.2 Study site - Porto Jofre, Mato Grosso Brasil*

This region is popularly known to be the best location in the world to observe and photograph wild jaguars and is considered a highly suitable habitat for jaguars due to its high productivity and prey abundance (both terrestrial and aquatic) (Tortato et al., 2017b). The high density of jaguars in the region  $4.08 \text{ individuals}/100 \text{ km}^2 \pm 0.73 \text{ SE}$  (Devlin et al., 2023) and the relative tranquility of individuals with human presence provided a rare opportunity to document the life of these elusive cats and to follow several lineages without the use of capturing or genetic sampling. The study site is in the most southern region of the state of Mato Grosso of the Northern Pantanal, located in the central west of Brazil, encompassing the village of Porto Jofre,

private properties and the Encontro das Águas State Park (Figure 2). In the summer (November-June) the region is classified as being warm and humid with high precipitation, and dry in the winter (July-October). Climate is described as tropical savanna with an average annual temperature between 25°C and 35°C and precipitation is 1,176 mm annually. Rainfall from surrounding areas outside the Pantanal largely controls the seasonal flooding, which is from January to June, with peak water levels in March. Therefore, the rainfall regime is the most important climatic variable (Bergier and Assine, 2016).

The vegetation type of the study site is divided into three different subdivisions based on landscape features such as flooding dynamics and hydroperiods, major rivers, and local names. The subdivisions are called São Lourenço North, São Lourenço South and Paiaguás (Padovani, 2010). The sampling took place each dry season (June-November) between three major rivers and its tributary; Cuiabá (-17.227210°, -56.681020°), Três Irmãos (-17.245806°, -56.653224°) and Piquiri (-17.340544°, -56.662902°) (Figure 2B). Each river has slightly different sediments and aquatic vegetation but the riverine edge is mainly composed of semi-deciduous forest formations and wooded savanna, with smaller patches of pasture and forested savanna, with mostly a clay and sand soil type (Moraes et al., 2021; Padovani, 2010). Dominant tree species in river corridors include *Attalea phalerata*, *Vochysia divergens*, *Handroanthus impetiginosus*, *Tabebuia aurea*, *Hymenaea stigonocarpa*, *Copernicia alba*, *Ficus insipida*, *Guazuma ulmifolia*, and *Cecropia pachystachya*.



**Figure 2:** A) Map of South America and the Brazilian Pantanal biome in green. B) Survey map showing the rivers (black) and location of where sampling occurred from 2013-2023. The yellow is the Encontro Das Águas State Park located in the state of Mato Grosso, Brazil.

### 2.3 Population sampling

From 2013 to 2024, we applied mark-recapture field procedures aimed to provide estimates of population parameters. During the dry season, from June to November, we conducted jaguar monitoring trips within the study area. The size of the combined navigable river system where the data was collected is ~203 km long (Figure 2B). We monitored this river system 3-5 days a week on average, attempting to cover the entire study area. It is not possible to survey the entire region in one day, therefore we divided it throughout the week, focusing on the principal rivers, Cuiabá and Três Irmãos every other day. We navigate on average 70 -100km

per day. Each year, the days spent per week were limited by funding for boat fuel, boat drivers, and lodging. We deployed three different methods to collect data: (1) surveying, where we searched for and recorded jaguars found independently; (2) tourism through the use of radio communication with tourism boats; (3) citizen science, where local guides, drivers, and tourists submitted jaguar sighting reports via a dedicated WhatsApp group or our website (<https://www.jaguaridproject.com/submit-your-photos>). Every year thousands of tourists visit this region to observe jaguars in the wild. During the peak tourism months June-October, an average of 30 boats are on the river daily looking for jaguars and other wildlife (Tortato et al., 2024). In this region there is a collaborative effort of searching for jaguars and a shared VHF radio channel to report sightings. We incorporated the variable number of days or sampling per year, in the capture probability modeling.

We collected the following information at each sighting: identification of individual, date, sex, GPS coordinates, start and end time of observation (see project site in detail <https://www.jaguaridproject.com/>). After collecting the data, we continued our route surveying the same river system year after year. We identified individual jaguars based on their unique spots and rosettes (Silver et al., 2004). Primary identification relied on the facial pattern between the forehead, while left and right flank patterns were also used when necessary (HARMSSEN, 2006). We conducted proper identification of the individual was conducted by visually matching images and confirming them with a complete dossier created by Jaguar Identification Project (Martin, 2024 unpublished work see supplemental material; (Martin, A., 2022). The dossier contains all jaguars photographed by researchers, tourists, boat drivers and tour guides since the beginning of tourism began in the region in 2004. The dossier also includes documented family lineages for each observed individual, noting whether they were first

identified as a cub or as an adult. This information helps estimate the individual's age and confirm their individual's sex when not immediately apparent during the time of the observation.

#### *2.4 Population modeling*

We analyzed the data using capture-mark-recapture (CMR) using the package *RMark* available in R language (R Core Team, 2022; White and Burnham, 1999) to estimate annual abundance, apparent survival, recruitment, and annual population growth. Due to the lack of data on dead recovery, it is impossible to determine whether individuals leave the study area or die, which is why survival estimates in this study are treated as apparent survival rather than true survival. The years in this case are considered the primary occasions and months are the secondary occasions, this way we can reduce the uneven nuisance in effort that might be caused by the different number of days per month the sampling took place. CMR models are useful because they account for imperfect detection (detectability) while estimating true population parameters. We then applied Huggins Robust Design (RD) model (Pollock 1982), in which data collected within years will be assumed as a closed population (for detectability and abundance estimation), and between years as open population (for survival and recruitment estimation). This model estimates capture probabilities for each individual, which can vary across sampling occasions and can be incorporate individual and environmental covariates that might affect capture probabilities, such as age, sex, time, or weather conditions. Specifically, we applied the RD with Pradel  $f$  parametrization (Pradel 1996) that allows us to estimate survival and recruitment between years. The  $f$  parameter represents the rate of recruitment (i.e., the addition of new individuals to the population) and is used alongside survival probabilities to provide a comprehensive understanding of population changes over time. This method helps in

distinguishing between losses due to mortality and gains due to new individuals, which is crucial for accurate population dynamics analysis. Abundance was estimated with the number of individuals not detected at each year  $f(0)$ . Population growth is not part of the model likelihood, but can be estimated as a derived parameter from abundance estimates for each year. RD with Pradel  $f$  parametrization was fitted under a Maximum Likelihood Estimation approach. For a complete description of the Huggins Robust Design model see (Huggins, 1991; HUGGINS, 1989).

First, we modeled the capture probability parameter by combining sex, age, year and effort to find the best model structure, while keeping constant the remaining parameters in the model (survival and recruitment). Once we found the best model structure we fixed it to run eight candidate models to test our hypothesis on population drivers of survival and recruitment, specifically looking for fire effects and if population parameters changes were aligned with our hypothesis. We included individual information such as sex (male and female), and age (cub and adult), as well as environmental information such as time (year of sampling), yearly rainfall, and wildfire event (before, during, after) as covariates to model the detection, survival and recruitment parameters. Years between 2013 and 2019 were considered before fire, 2020 was considered during fire, and years between 2021 and 2023 were considered after fire.

We then built eight models, and depicted different hypothesis on how recruitment and survival could respond to biological individual attributes (sex and age), environmental productivity and prey abundance (rainfall), years idiosyncrasies (year identity), and wildfire event (before, during, after):

- (1) Model Time: survival and recruitment change between years due to year idiosyncrasies.

- (2) Model Jaguar Biology: sex and age affects survival and recruitment. Females have smaller territories and reduced need for territorial disputes and usually a more stable resource access, while males face higher mortality risks due to territorial conflicts and dispersal. Cubs face high vulnerability due to inexperience and dependence on their mothers. Females have key roles in recruitment through reproduction and cub-rearing where subadult males contribute to recruitment because of their higher tendency to disperse. The recruitment of cubs into the adult population depends on cub survival which is influenced by ecological conditions and parental care.
- (3) Model Rainfall: survival and recruitment correlate quadratically with rainfall. Generally rainfall informs productivity and prey abundance, but very high and prolonged flooding can also impair individual movement and prey access.
- (4) Model Fire: survival and recruitment is different before, during and after fire. Before fire there should be stable conditions in terms of habitat and resources. During fire there are immediate threats from displacement and injury and after fire a loss of habitat and prey availability.
- (5) Model Jaguar Biology and Time Combination: sex and age between the years affects survival and recruitment. Population dynamics has a response over temporal scales and yearly idiosyncrasies. This model incorporates life stages with time dependent transitions.
- (6) Model Jaguar Biology with Rainfall Combination: rainfall can influence jaguar biology by affecting survival and recruitment through changes in vegetation, prey

abundance and habitat quality which impacts jaguars differently based on their sex and age.

(7) Model Jaguar Biology with Fire Combination: sex and age during each stage of fire (before, during and after) will have affects survival and recruitment of the population.

(8) Model Jaguar Biology with Rainfall and Fire Combination: sex and age with rainfall and fire affects survival and recruitment. Comprehensive model to understand how these two critical environmental factors interact with biological traits like sex and age, influencing survival and recruitment.

Monthly rainfall data was collected from three stations located at municipalities surrounding the studied area (cities of Caceres, Cuiabá and Corumbá), and averaged to represent. Data was collected and held by the Brazilian Meteorology Institute, and can be downloaded at <https://portal.inmet.gov.br/>. We included effects of rainfall on survival and recruitment in the model as yearly accumulated rainfall with one year delay. For instance, survival/recruitment from year 1 [sampled between June to November] to year 2 [June to November] was modeled as affected by the rainfall accumulated between October of year 1 and June of year 2 (the flooding season between sampled years). We ranked the candidate models according to the corrected Akaike Information Criterion (AICc) values (Burnham and Anderson 2002), in which models with the lowest score are considered the best model for a given data set. Models with  $\Delta AICc$  value equal or less than 2.00 are also considered with good support and averaged to obtain covariates coefficients and highlighting the direction and magnitude of covariates effects.

### **3. Results**

### *3.1 Sampling effort and Population Trends*

During the 11 years (2013-2023), we recorded 4,161 jaguar sightings, totaling 270 individuals (130 males, 118 females, 22 with unknown sex) of which 189 first spotted as adults and 81 as cubs. Forty of the individuals initially sighted as cubs were followed through their adulthood. Per year, the average number of captures was 376. Females were observed on average 19 times (median = 6, range = 1-270) and males 13 times (median = 3, range = 1-140). The average time range between first and last captures per individual was 18 months (median = 4.8, range = 0-128), in which females presented average time range of 64 months (median = 54, range = 0-128), and males 34 months (median = 29, range = 0-86).

### *3.2. Model selection and population estimates*

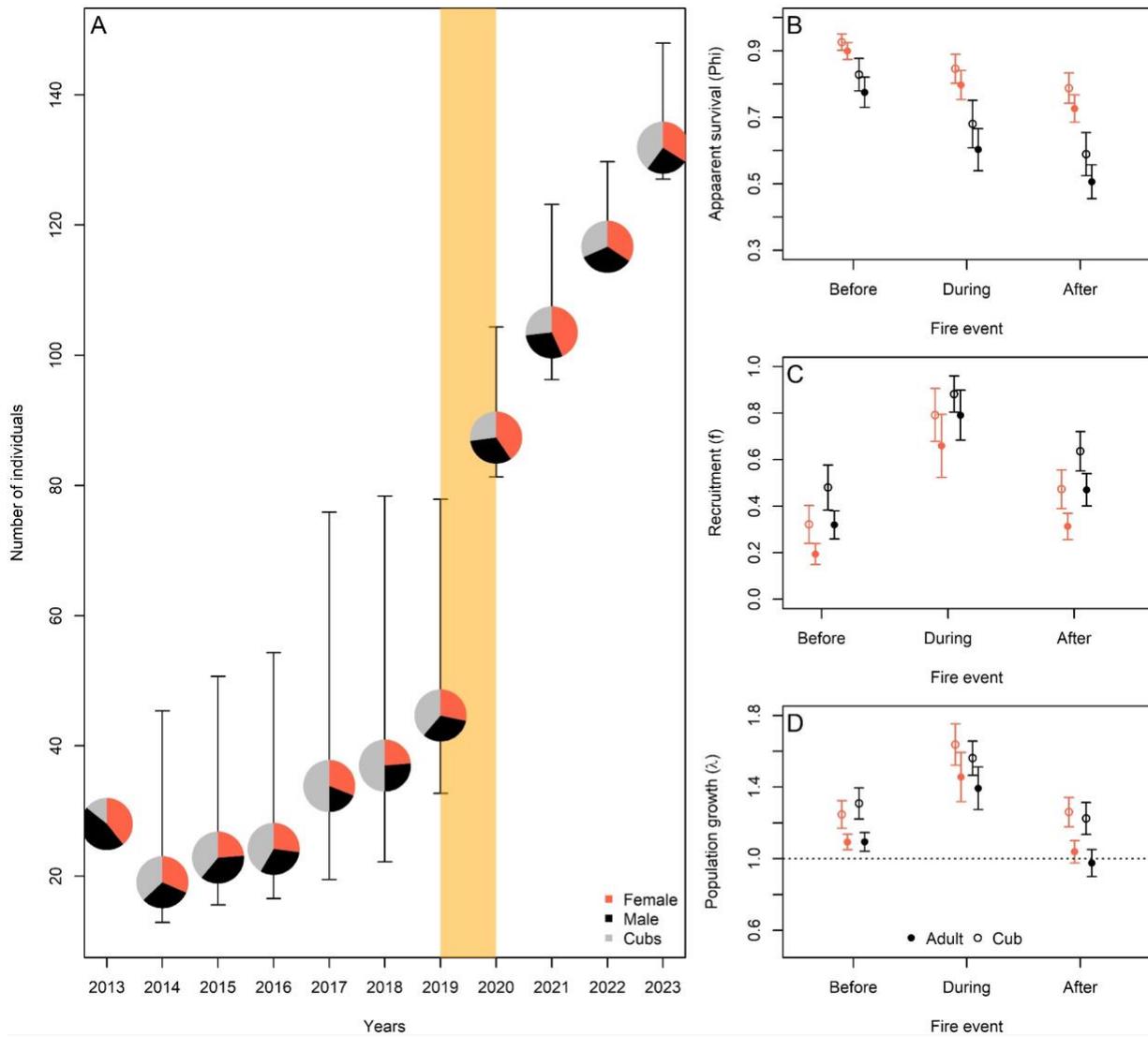
Regarding capturability and re-capturability, 5 models received strong support ( $\Delta AICc < 2$ ; summed  $w = 0.85$ ; Table S1). The best ranked model ( $w = 0.40$ ) included year idiosyncrasies and jaguar age affecting both captures and recaptures. However, the third best ranked model also included sex affecting capturability ( $\Delta AICc = 1.22$ ;  $w = 0.21$ ) and the fourth best included the sex effect also on re-capturability ( $\Delta AICc = 1.24$ ;  $w = 0.08$ ). Therefore, we fixed the covariates sex, age, and year affecting both capturability and re-capturability to compare the eight candidate models. Overall, capturability varied across years from 0.09 to 0.51, while re-capturability tended to be higher (0.11 to 0.70). Cubs were easier to capture and recapture than adults ( $\beta_{\text{capture}} = 0.21$ ; 95% CI = 0.03 – 0.44 and  $\beta_{\text{recapture}} = 0.75$ ; 95% CI = 0.54 – 0.97), while males tended to be less detectable than females, but coefficients of effect crossed zero ( $\beta_{\text{capture}} = -0.09$ ; 95% CI = -0.29 – 0.10 and  $\beta_{\text{recapture}} = 0.09$ ; 95% CI = -0.10 – 0.29).

Results for sampling effort when combining the three different methods over the 11 years of collecting information showed that sampling effort had no measurable effect on capturability (0.00; 95% CI= -0.81 –0.82) (Table 2).

Of the eight models to test our hypothesis, the best-fit model ( $w = 0.89$ ) was the “Model Jaguar Biology with Fire Combination” including the covariates for jaguar biology (sex and age) and fire as the main drivers of survivorship and recruitment (Table 1). The second-best model was the “Model Jaguar Biology with Rainfall and Fire Combination” just adding the quadratic effect of rainfall ( $\Delta AIC = 2.00$ ;  $w = 0.10$ ), and together with the first model held 99% of all support, indicating the high importance of fire on population dynamics of jaguars (Table 1, Table 2). According to these two top models, males presented lower survival and higher recruitment than females (Figure 3B,C; Table 2), while cubs presented non-significant higher survival and significantly higher recruitment than adults (Figure 3B,C; Table 2). When compared to the stage before fire (overall values ranged 0.80-0.96), survival dropped during fire (0.60-0.85), and dropped even more after fire (0.50-0.78) (Figure 3B,C; Table 2), while recruitment dramatically increased during fire, decreasing after fire (from around 0.30 to 0.80), and tending to reach similar figures to those observed at the stage before fire (Figure 3B,C; Table 2). The combination of estimated population entries (recruitment), and exits (apparent survival) indicated a strong population growth of males, females, cubs and adults during the fire stage (from 15% [ $\lambda = 1.15$ ] to about 50% [ $\lambda = 1.5$ ] of annual population increase), with sequential decrease and return to values observed before fire, mainly for adults (Figure 3D). Note, even though survival decreased during fire, the population growth had a steep increase related to both influx of new adults, and also cubs, indicating that local reproduction boosted despite fire. As a result, estimated jaguar abundance on riverine doubled to tripled immediately

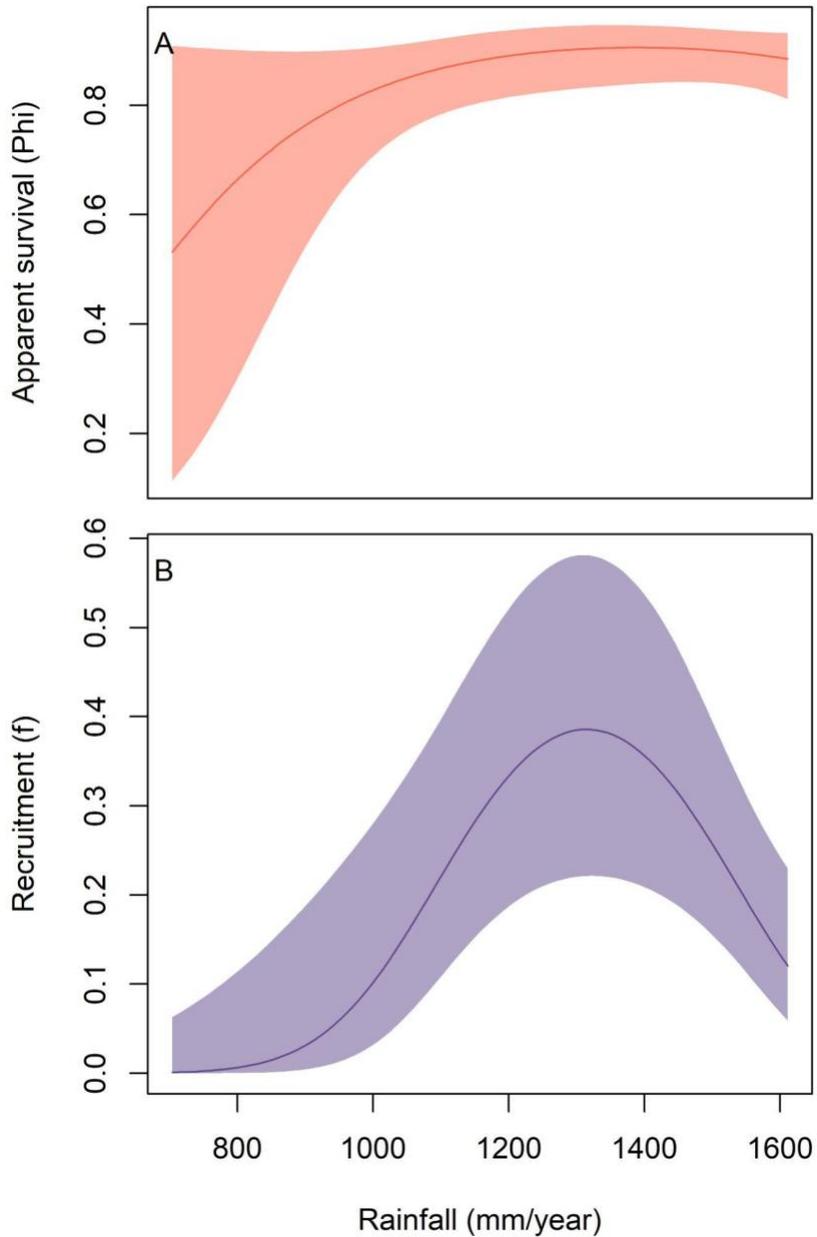
after the fire event (from about 40 to 90 individuals; Figure 3A), with a slight increase in proportion of females composing the population.

Considering the quadratic rainfall effect supported by the second-best model, survival had a positive linear effect on survival (Table 3, Figure 3), and the recruitment presented a quadratic shape with rainfall, picking up around 1200-1400mm of accumulated rainfall (Table 3, Figure 3). Recruitment sharply dropping down at extremes ( $< 1000\text{mm}$  or  $> 1500\text{mm}$ ), mainly for the driest years (Figure 3 - right tail).



**Figure 3.** Demographic estimation of the best ranked population model (Biology+Fire model; Table 1) derived from twelve years of population dynamics of jaguars (*Panthera*

*onca*) crossing an extreme fire event in the Northern Pantanal of Mato Grosso, Brazil. (A) Estimated number of individuals through time. Whiskers indicate 95% confidence intervals. Pie charts indicate the sex and age structure of the population (males in black, females in red, cubs in gray). Vertical orange shade indicates the extreme fire event. (B) Apparent survivorship, (C) recruitment, and (D) population growth of jaguars before, during and after the extreme fire event. Solid red dots indicate adult females, solid black males, open red cub females, and open black dots indicate cub males. The results were based on the best ranked model presented in Table 1.



**Figure 4.** Effects of accumulated annual rainfall on jaguar yearly apparent survival probability (A) and recruitment probability (B), considering the second best ranked

model (Biology+Fire+Rainfall) ( $\Delta AIC = 2.00$ ; Table 1) in the Northern Pantanal of Mato Grosso, Brazil.

**Table 1.** Population model ranking using Huggins Robust Design with Pradel parametrization. Estimated parameters: *Phi* (apparent survival), *f* (recruitment), *p* (capturability) and *c* (re-capturability). *k* depicts number of parameters, deviance the likelihood, AICc corrected Akaike Information Criteria,  $\Delta$ AICc the difference between the current and the best model, and *w* model weight.

<b>Model</b>	<b><i>Phi</i> and <i>f</i></b>	<b><i>p</i> and <i>c</i></b>	<b>k</b>	<b>Deviance</b>	<b>AICc</b>	<b><math>\Delta</math>AICc</b>	<b>w</b>
Fire and jaguar biology	fire + sex+ age	effort + session + sex + age	49	1932.04	4209.81	0	0.89
Fire, rain and jaguar biology	fire + sex + age + quadratic rain	effort + session + sex + age	53	1923.53	4209.96	2.00	0.10
Time and jaguar biology	time + sex + age	effort + session + sex + age	63	1912.83	4221.18	11.37	<0.01
Fire	fire	effort + session + sex + age	45	1955.42	4224.57	14.77	<0.01
Rain and jaguar biology	sex + age + quadratic rain	effort + session + sex + age	49	1949.36	4227.12	17.31	<0.01
Jaguar biology	ages + sex	effort + session + sex + age	45	1963.91	4233.06	23.25	<0.01
Time	time	effort + session + sex + age	59	1938.1	4237.64	27.84	<0.01
Rain	quadratic rain	effort + session + sex + age	45	1972.09	4241.24	31.43	<0.01

**Table 2.** Estimated covariates effect (and their 95% confidence intervals) on population parameters for the two best ranked models ( $w = 0.99$ ).

Parameter	Covariate	Coefficient	Model	
			Fire and jaguar biology	Fire, jaguar biology and rain
Survival ( $\Phi$ )	Intercept	2.03	2.03 (1.51,2.55)	-6.5 (-17.24, 4.24)
	During fire	-0.82	-0.82 (-1.52,-0.12)	0.86 (-1.15, 2.86)
	After fire	-1.19	-1.19 (-1.76,-0.63)	-1.09 (-1.63, -0.54)
	Sex <sub>male</sub>	-0.69	-0.69 (-1.11,-0.28)	-0.7 (-1.12, -0.29)
	Age <sub>cub</sub>	0.30	0.30 (-0.2,0.81)	0.3 (-0.21, 0.8)
	Rain	—	—	0.008 (0.004, 0.03)
	Rain <sup>2</sup>	—	—	0.0005 (-0.0001, 0.0001)
Recruitment ( $f$ )	Intercept	-1.37	-1.37 (-1.94,-0.81)	-30.36 (-50.05, -10.68)
	During fire	2.20	2.20 (0.69,3.7)	6.74 (2.56, 10.92)
	After fire	0.63	0.63 (-0.01,1.28)	0.95 (0.18, 1.71)
	Sex <sub>male</sub>	0.50	0.50 (-0.01,1.02)	0.56 (0.02, 1.09)
	Age <sub>cub</sub>	0.71	0.71 (0.07,1.34)	0.73 (0.08, 1.39)
	Rain	—	—	0.05 (0.04, 0.06)

	Rain <sup>2</sup>	—	—	-0.002(-0.001— -0.003)
Capturability	Intercept	-0.44	-0.44 (-79.21,78.33)	-0.45 (-0.45— -0.45)
	Sex <sub>male</sub>	-0.05	-0.05 (-0.24,0.14)	-0.03 (-0.23—0.16)
	Age <sub>cub</sub>	0.09	0.09 (-0.14,0.32)	0.09 (-0.14—0.32)
	Effort	0.00	0.00 (-0.81,0.82)	0.003(0.002—0.004)

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#### 4. Discussion

Our study represents one of the longest and most comprehensive study on a threatened long-lived felid, uniquely assessing the impact of wildfires on their demographic dynamics, and confirming the role of riverine habitats as refuges. A few studies have investigated the impact of wildfires on jaguars in the Pantanal (Bardales et al., 2024; De Barros et al., 2022) but none have so far assessed the effects on long term jaguar population demographics. Unlike other long-term studies, our analysis explicitly estimates rare population parameters such as survival and recruitment within the same model, while incorporating individual covariates (sex and age) and environmental factors such as rainfall and fire effects. This approach allows us to evaluate critical questions about how riverine forests act as refuges during disturbances, buffering fire impacts, safeguarding reproductive individuals and facilitating the repopulation of burned areas. These findings build upon earlier studies, such as Robinson et al. (2013) and Bardales et al (2024), emphasizing the central role of refuges in sustaining jaguar populations under increasing environmental pressures and climate change.

Before the mega fire of 2020, our estimated survival (about 0.80) and recruitment (around 0.30) rates were values that align closely with the findings from the few other long-term studies on jaguars. For instance, survival rates at the Cockscomb Basin Wildlife Sanctuary in Belize were reported as 0.78, and at Emas National Park in the Brazilian Cerrado as 0.77, both comparable to our estimates (Alves et al., 2024; Harmsen et al., 2017). However, survival rates at The Northern Jaguar Reserve in Sonora Mexico (0.47 to 0.56) were notably lower, possibly due to increased anthropogenic pressures (Gutiérrez-González et al., 2015). In the Colombian Llanos, survival rates were similar between sexes (males: 0.783; females: 0.798), and similar to

our estimates (Hyde et al., 2023). Our recruitment values were most comparable to values observed in Colombian Llanos (0.30) and in Belize (0.28) (Harmsen et al., 2017; Hyde et al., 2023). In Emas National Park recruitment was lower (0.19), likely limited by habitat isolation caused by surrounding highways (Alves et al., 2024). These comparisons highlight the variability in demographic parameters across jaguar populations and underscore the importance of contextual factors such as habitat connectivity and anthropogenic influences.

Sex and age-specific survival and recruitment findings in other *Panthera* species and smaller felids are sparsely available but offer valuable comparative insights. For instance, studies on leopards (*Panthera pardus*) show similar high survival rates for adults and cubs (0.94 and 0.80 respectively) in protected areas (Swanepoel et al., 2015), but much lower recruitment rates for males (0.04) than females (0.24) (Rostro-García et al., 2023), when compared to our pre-fire results. Whereas snow leopards (*Panthera uncia*) exhibited comparable survival across sexes and ages (adults:  $0.83 \pm 0.07$ ; cubs:  $0.83 \pm 0.15$ ) (Sharma et al., 2014). Similar findings were observed in lions (*Panthera leo*), where survival rates were shown to be influenced by habitat choice (0.88-0.82) and dry and wet seasonality (wet: 0.94-0.89; dry: 0.92-0.98), also depending on the size of the pride (Conquet et al., 2024). Smaller felids also exhibit similar variability in survival and recruitment across sex and age classes. Survival for female ocelots (*Leopardus pardalis*) was 0.81–0.87; whereas for males 0.73–0.87. In contrast to our results, female ocelots have higher recruitment (0.09–0.12) than males (0.06–0.08) (Satter et al., 2019). Bobcats (*Lynx rufus*) showed lower but comparable survival rates for females (0.79) and juveniles (0.77) (Lehman et al., 2024). Among these studies survival rates for both large and small felids appear relatively consistent, typically ranging from above 75% to lower 90% range. Recruitment, however, shows greater variability, likely driven by site specific pressures. The global similarity in survival rates

likely reflects shared biological, ecological, and evolutionary traits that influence felid life history strategies. Our work stands apart as the only to address both survival and recruitment across all demographic groups. By capturing these metrics in a context of disturbance impacted ecosystem, our findings provide new insights into how such pressures might shape populations and offer broader implications for felid conservation.

Our study proved compelling evidence that riverine forests serve as critical refuges during extreme fire events, directly influencing survival and recruitment dynamics across all age and sex groups. Before the fire, stable survival and recruitment rates highlight the suitability of these habitats under normal conditions. During the fire, recruitment surged, particularly among males and juveniles, as displaced individuals sought refuge in the riverine forest. This influx temporarily stabilized the population, demonstrating the buffering capacity of these habitats. Post-fire, survival rates declined due to heightened competition for resources and density-dependent effects, while recruitment decreased, stabilizing below the pre-fire peak but higher than initial levels. These patterns align with our hypothesis, as depicted in Figure 1, emphasizing the role of the refuge in preserving reproductive individuals and facilitating population recovery. One of the only other studies on wildfire and *Panthera* species that can be comparable to ours is by (Eby et al., 2013), who observed that burning does not negatively impact lion (*Panthera leo*) fitness. However, their study did not investigate this phenomenon in the same demographic detail as ours. They suggested that the lack of impact might be linked to the heterogeneity of the burned areas across the landscape. We therefore attribute our findings to the fire refuge provided by the riverine forests, which created spatial heterogeneity between burned and unburned areas as proposed by Eby et al. (2013). Uniquely, our study measures how these riverine systems

operate to safeguard jaguar populations by offering detailed insights into the survival and recruitment dynamics of each demographic group.

An unexpected finding in this study was the substantial increase in the number of cubs during and after the fire. This could be attributed to the riverine forest acting not only as a crucial refuge during the fire but also becoming an optional environment for reproduction. The riverine habitat likely provided ample prey compared to the fire-torn environments outside the major waterways. However, this pattern contrasts with our hypothesis and previous research. For instance, research on black bears in central Arizona (Cunningham and Ballard, 2006) found that high intensity wildfires negatively impacted reproduction, with the burned forest showing the lowest reproductive success compared to their unburned reference site and the same area 20 years prior to the fire. Additionally, cub recruitment to the yearling age class was significantly reduced in the burned areas. These findings suggest that fire intensity and its effect on habitat can disrupt reproductive dynamics, particularly in species with fewer refuge options.

While the observed influx of displaced individuals into riverine refuges highlights the critical role these habitats play during extreme fire events, heightened densities may also introduce challenges to population persistence. Increased competition for limited prey and habitat resources can negatively affect survival and reproduction, particularly for cubs and subordinate individuals (Tortato et al., 2017a). Additionally, crowded conditions may elevate the risk of disease transmission and stress-induced mortality, potentially counteracting the short-term demographic benefits of refuges (Cunningham et al., 2021). These density-dependent effects could lead to delayed population recovery in both refuge and surrounding areas as individuals disperse back to recovering habitats. Such effects and negative density dependence underscore

the need for careful management of refuge to mitigate long-term impacts and maintain population resilience (Crooks et al., 2011; Robinson et al., 2013).

Despite the comprehensive and empirical nature of this study, our reliance on observational data and limitation to the riverine habitat limits the generalizability of our findings to jaguar populations outside of these specific areas. Further research should assess demographic parameters and the impact of fires in non-refuge habitats, as well as continue tracking the post-fire period to understand the effects of successive, accumulated fire events over multiple years. While river margins are crucial habitats (Quigley and Crawshaw, 1992), their representativeness of the broader local population remains a key question. Current studies are already underway with an aim to expand the scope beyond riverine forest to include a broader range of habitats, providing a more complete understanding of jaguar population dynamics across different landscapes that will further enhance our understanding of jaguar resilience in the face of increasing threats in the Pantanal.

### **Conservation Implications:**

The importance of this long-term population monitoring cannot be overstated. It allows conservation managers to identify when action is needed and avoids pitfalls of short-term studies that may lead to incorrect conclusions (Lebreton et al., 1992; White, 2019). Our findings underscore the importance of long-term monitoring, refuge habitat conservation, and proactive measures such as fire prevention, early detection and effective management in mitigating the effects of wildfire on jaguar populations (Bardales et al., 2024; De Barros et al., 2022). This was first proposed by Quigley and Crawshaw (1992), who even before the current

day climate crises, suggested that conservation strategies should prioritize maintaining and restoring riverine forest to mitigate the uncertainty of demographic and genetic pressures on jaguars. Likewise, restoration efforts can play a critical role in maintaining these ecosystems, while tourism may serve as a vital incentive to conserve jaguars and the habitats they depend on, such as these riverine forests (Tortato et al., 2017b). These efforts are essential for ensuring the persistence of the iconic species in a rapidly changing environment.

The findings highlight the importance of preserving these refuge habitats for jaguars, especially in regions prone to extreme weather events. However, recent local threats such as infrastructure development and chemical deforestation in the region, pose new challenges, killing vegetation, contaminating soils, polluting rivers and potentially affecting groundwater. These new threats further emphasize the urgent need for stricter enforcement of conservation laws such as the Brazilian Forest Code (Law No. 12.651/2012). The Brazilian Forest Code mandates the preservation of native vegetation along watercourses to safeguard biodiversity, water resources, and soil stability but exceptions may be granted for activities deemed of public utility, social interest, or low environmental impact. However Silva et al. (2017) has shown that the Forest Code has actually lessened the legal responsibility of the rural owners in relation to the maintenance of forest fragments in their properties. As recently as 2024, chemical deforestation was used to kill 300 square miles of forested area along the Cuiaba river just north of our study region (“The New Threat to Brazil’s Forests: Chemicals - The New York Times,” n.d.). Coordination with local governments is crucial to ensure that development activities, such as proposed road construction, do not conflict with conservation objectives. It's been demonstrated that jaguar density is significantly higher in remote areas than in more accessible ones, showcasing that when roads appear, jaguars decrease (Espinosa et al., 2018). After

wildfires in North America, mountain lions increased behaviors associated with anthropogenic risk, including more frequent road and freeway crossings and higher diurnal activity (Blakey et al., 2022). These studies supplement the need for planned human adaptation strategies that integrate conservation with infrastructure development in the Pantanal.

## **5. Conclusion**

Our study demonstrates the critical need to preserve riverine systems as refuges to support jaguar populations during extreme disturbances such as wildfires. Enforcement of conservation laws and the restoration of critical habitats as refuges are essential to ensure the long-term survival of jaguars. Additionally, understanding the dynamics of post-fire population recovery for jaguars can inform management practices aimed at supporting other large predator populations through extreme fire events and threats.

This interplay of fire, habitat, and exposure to risk may also explain the greater visibility of jaguars along riverbanks. While riverine forests offer refuge and resources, they may simultaneously leave females and cubs with fewer choices for secluded, undisturbed environments. In areas like Porto Jofre, where tourism plays a protective role, this increased exposure may not result in heightened mortality. However, in regions lacking similar safeguards, the exposure of cubs and their mothers to human activities along river banks could lead to greater post-fire predation and anthropogenic impacts such as hunting, road collisions and conflict-driven killings.

Overall, these patterns underscore the complex, context dependent effects of fire on wildlife and the need to consider both ecological and anthropogenic factors in post-fire

management and conservation. Future research should aim to broaden the scope of monitoring efforts, identifying and maintaining ecological refuge to encompass diverse habitats, providing a comprehensive understanding of jaguar population dynamics and providing resilience in the face of climate change.

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## Supplementary Material

Table S1. Model Selection regarding capturability and re-capturability

Phi	f	p	c	f0	model	npar	AICc	$\Delta$ AICc	weight	Deviance
~1	~1	~session + initial.age.class	~session + initial.age.class	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~session + initial.age.class)f0(~session)	37	3829.96912	0	0.09575531	2086.609
~1	~1	~session	~session + initial.age.class	~session	Phi(~1)f(~1)p(~session)c(~session + initial.age.class)f0(~session)	36	3830.66502	0.69589463	0.06761628	2089.4349
~1	~1	~session + sex + initial.age.class	~session + initial.age.class	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~session + initial.age.class)f0(~session)	38	3831.19431	1.22519033	0.05189389	2085.7007
~1	~1	~session + initial.age.class	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~session + sex + initial.age.class)f0(~session)	38	3831.21371	1.24459033	0.05139295	2085.7201
~1	~1	~session + sex	~session + initial.age.class	~session	Phi(~1)f(~1)p(~session + sex)c(~session + initial.age.class)f0(~session)	37	3831.62262	1.6535	0.04188996	2088.2625
~1	~1	~session	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~session)c(~session + sex + initial.age.class)f0(~session)	37	3831.90602	1.9369	0.03635552	2088.546
~1	~1	~session + sex + initial.age.class	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~session + sex + initial.age.class)f0(~session)	39	3832.4427	2.47357519	0.02779924	2084.8117
~1	~1	~citzen + session	~session + initial.age.class	~session	Phi(~1)f(~1)p(~citzen + session)c(~session + initial.age.class)f0(~session)	37	3832.79492	2.8258	0.02331032	2089.4349

~1	~1	~session + sex	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~session + sex)c(~session + sex + initial.age.class)f0(~session)	38	3832.86721	2.89809033	0.02248281	2087.3736
~1	~1	~session + citizen + initial.age.class + sex	~session + initial.age.class	~session	Phi(~1)f(~1)p(~session + citizen + initial.age.class + sex)c(~session + initial.age.class)f0(~session)	39	3833.3316	3.36247519	0.01782423	2085.7007
~1	~1	~citizen + session	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + session)c(~session + sex + initial.age.class)f0(~session)	38	3834.03961	4.07049033	0.01251028	2088.5459
~1	~1	~session + citizen + initial.age.class + sex	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~session + citizen + initial.age.class + sex)c(~session + sex + initial.age.class)f0(~session)	40	3834.58369	4.61456419	0.00953066	2084.8117
~1	~1	~session + initial.age.class	~initial.age.class	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~initial.age.class)f0(~session)	27	3843.55773	13.5886063	0.00010726	2121.3325
~1	~1	~session	~initial.age.class	~session	Phi(~1)f(~1)p(~session)c(~initial.age.class)f0(~session)	26	3844.23665	14.2675313	7.6384955775636e-05	2124.1049
~1	~1	~session + sex + initial.age.class	~initial.age.class	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~initial.age.class)f0(~session)	28	3844.7672	14.7980724	5.8587139991534e-05	2120.4447
~1	~1	~session + sex	~initial.age.class	~session	Phi(~1)f(~1)p(~session + sex)c(~initial.age.class)f0(~session)	27	3845.15783	15.1887063	4.81922514620709e-05	2122.9325
~1	~1	~citizen + session	~initial.age.class	~session	Phi(~1)f(~1)p(~citizen + session)c(~initial.age.class)f0(~session)	27	3846.33013	16.3610063	2.6817328116352e-05	2124.1049
~1	~1	~session + citizen + initial.age.class + sex	~initial.age.class	~session	Phi(~1)f(~1)p(~session + citizen + initial.age.class + sex)c(~initial.age.class)f0(~session)	29	3846.86806	16.8989387	2.04929729454334e-05	2120.4449
~1	~1	~citizen + initial.age.class	~session + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + initial.age.class)c(~session + initial.age.class)f0(~session)	28	3867.0792	37.1100724	8.37168844870302e-10	2142.7567

~1	~1	~citizen	~session + initial.age.class	~session	Phi(~1)f(~1)p(~citizen)c(~session + initial.age.class)f0(~session)	27	3868.00653	38.0374063	5.26556589405318e-10	2145.7812
~1	~1	~citizen + initial.age.class	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + initial.age.class)c(~session + sex + initial.age.class)f0(~session)	29	3868.29096	38.3218387	4.56752926378006e-10	2141.8678
~1	~1	~citizen + initial.age.class + sex	~session + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + initial.age.class + sex)c(~session + initial.age.class)f0(~session)	29	3868.95056	38.9814387	3.28436199759307e-10	2142.5274
~1	~1	~citizen	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~citizen)c(~session + sex + initial.age.class)f0(~session)	28	3869.2147	39.2455724	2.87802872816998e-10	2144.8923
~1	~1	~citizen + sex	~session + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + sex)c(~session + initial.age.class)f0(~session)	28	3869.5675	39.5983724	2.41260141440432e-10	2145.245
~1	~1	~citizen + initial.age.class + sex	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + initial.age.class + sex)c(~session + sex + initial.age.class)f0(~session)	30	3870.16594	40.1968146	1.78869170207027e-10	2141.6384
~1	~1	~citizen + sex	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~citizen + sex)c(~session + sex + initial.age.class)f0(~session)	29	3870.77926	40.8101387	1.3162969011151e-10	2144.3561
~1	~1	~session + initial.age.class	~session	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~session)f0(~session)	36	3877.58992	47.6207946	4.36957019497512e-12	2136.3598
~1	~1	~session	~session	~session	Phi(~1)f(~1)p(~session)c(~session)f0(~session)	35	3878.28959	48.3204647	3.07969211197082e-12	2139.1857
~1	~1	~session + sex + initial.age.class	~session	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~session)f0(~session)	37	3878.81152	48.8424	2.3723047798369e-12	2135.4514
~1	~1	~session + sex	~session	~session	Phi(~1)f(~1)p(~session + sex)c(~session)f0(~session)	36	3879.24342	49.2742946	1.91155041946624e-12	2138.0133

~1	~1	~session + initial.age.class	~session + sex	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~session + sex)f0(~session)	37	3879.54592	49.5768	1.643226954 19849e-12	2136.1858
~1	~1	~session	~session + sex	~session	Phi(~1)f(~1)p(~session)c(~session + sex)f0(~session)	36	3880.24182	50.2726946	1.160341839 25386e-12	2139.0117
~1	~1	~citzen + session	~session	~session	Phi(~1)f(~1)p(~citzen + session)c(~session)f0(~session)	36	3880.41582	50.4466946	1.063658787 14887e-12	2139.1857
~1	~1	~session + sex + initial.age.class	~session + sex	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~session + sex)f0(~session)	38	3880.77111	50.8019903	8.905347069 45473e-13	2135.2775
~1	~1	~citzen + initial.age.class	~initial.age.class	~session	Phi(~1)f(~1)p(~citzen + initial.age.class)c(~initial.age.class)f0(~session)	18	3880.93803	50.9689091	8.192281942 70257e-13	2177.4267
~1	~1	~session + citzen + initial.age.class + sex	~session	~session	Phi(~1)f(~1)p(~session + citzen + initial.age.class + sex)c(~session)f0(~session)	38	3880.94511	50.9759903	8.163327687 23306e-13	2135.4514
~1	~1	~session + sex	~session + sex	~session	Phi(~1)f(~1)p(~session + sex)c(~session + sex)f0(~session)	37	3881.19942	51.2303	7.188604447 15719e-13	2137.8393
~1	~1	~citzen	~initial.age.class	~session	Phi(~1)f(~1)p(~citzen)c(~initial.age.class)f0(~session)	17	3881.90087	51.9317425	5.062071583 76621e-13	2180.4512
~1	~1	~citzen + session	~session + sex	~session	Phi(~1)f(~1)p(~citzen + session)c(~session + sex)f0(~session)	37	3882.37182	52.4027	4.000010781 66147e-13	2139.0117
~1	~1	~citzen + initial.age.class + sex	~initial.age.class	~session	Phi(~1)f(~1)p(~citzen + initial.age.class + sex)c(~initial.age.class)f0(~session)	19	3882.77381	52.804685	3.271683079 64477e-13	2177.1974
~1	~1	~session + citzen + initial.age.class + sex	~session + sex	~session	Phi(~1)f(~1)p(~session + citzen + initial.age.class + sex)c(~session + sex)f0(~session)	39	3882.9084	52.9392752	3.058759557 52375e-13	2135.2775
~1	~1	~initial.age.class	~session + initial.age.class	~session	Phi(~1)f(~1)p(~initial.age.class)c(~session + initial.age.class)f0(~session)	27	3882.97033	53.0012063	2.965494806 66362e-13	2160.745

~1	~1	~citizen + sex	~initial.age.class	~session	Phi(~1)f(~1)p(~citizen + sex)c(~initial.age.class)f0(~session)	18	3883.42633	53.4572091	2.360899013 77365e-13	2179.915
~1	~1	~initial.age.class	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~initial.age.class)c(~session + sex + initial.age.class)f0(~session)	28	3884.1785	54.2093724	1.620866478 27459e-13	2159.8561
~1	~1	~1	~session + initial.age.class	~session	Phi(~1)f(~1)p(~1)c(~session + initial.age.class)f0(~session)	26	3886.91385	56.9447313	4.128303330 90381e-14	2166.7822
~1	~1	~1	~session + initial.age.class	~session	Phi(~1)f(~1)p(~1)c(~session + initial.age.class)f0(~session)	26	3886.91385	56.9447313	4.128303330 90381e-14	2166.7822
~1	~1	~1	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~1)c(~session + sex + initial.age.class)f0(~session)	27	3888.11853	58.1494063	2.260371078 96386e-14	2165.8932
~1	~1	~sex	~session + initial.age.class	~session	Phi(~1)f(~1)p(~sex)c(~session + initial.age.class)f0(~session)	27	3888.89793	58.9288063	1.530858966 73765e-14	2166.6727
~1	~1	~sex	~session + sex + initial.age.class	~session	Phi(~1)f(~1)p(~sex)c(~session + sex + initial.age.class)f0(~session)	28	3890.1062	60.1370724	8.366880001 87357e-15	2165.7837
~1	~1	~session + initial.age.class	~1	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~1)f0(~session)	26	3893.19715	63.2280313	1.783899323 94158e-15	2173.0654
~1	~1	~session	~1	~session	Phi(~1)f(~1)p(~session)c(~1)f0(~session)	25	3893.93296	63.9638381	1.234786649 24135e-15	2175.8913
~1	~1	~session + sex + initial.age.class	~1	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~1)f0(~session)	27	3894.38233	64.4132063	0	2172.157
~1	~1	~session + sex	~1	~session	Phi(~1)f(~1)p(~session + sex)c(~1)f0(~session)	26	3894.85055	64.8814313	0	2174.7189
~1	~1	~session + initial.age.class	~sex	~session	Phi(~1)f(~1)p(~session + initial.age.class)c(~sex)f0(~session)	27	3895.10013	65.1310063	0	2172.8748

~1	~1	~session	~sex	~session	Phi(~1)f(~1)p(~session)c(~sex)f0(~session)	26	3895.83235	65.8632313	0	2175.7007
~1	~1	~citizen + session	~1	~session	Phi(~1)f(~1)p(~citizen + session)c(~1)f0(~session)	26	3896.02295	66.0538313	0	2175.8913
~1	~1	~session + sex + initial.age.class	~sex	~session	Phi(~1)f(~1)p(~session + sex + initial.age.class)c(~sex)f0(~session)	28	3896.3627	66.3935724	0	2172.0403
~1	~1	~session + citizen + initial.age.class + sex	~1	~session	Phi(~1)f(~1)p(~session + citizen + initial.age.class + sex)c(~1)f0(~session)	28	3896.4795	66.5103724	0	2172.157
~1	~1	~session + sex	~sex	~session	Phi(~1)f(~1)p(~session + sex)c(~sex)f0(~session)	27	3896.75353	66.7844063	0	2174.5283
~1	~1	~initial.age.class	~initial.age.class	~session	Phi(~1)f(~1)p(~initial.age.class)c(~initial.age.class)f0(~session)	17	3896.86467	66.8955425	0	2195.415
~1	~1	~citizen + session	~sex	~session	Phi(~1)f(~1)p(~citizen + session)c(~sex)f0(~session)	27	3897.92593	67.9568063	0	2175.7007
~1	~1	~session + citizen + initial.age.class + sex	~sex	~session	Phi(~1)f(~1)p(~session + citizen + initial.age.class + sex)c(~sex)f0(~session)	29	3898.46386	68.4947387	0	2172.0406
~1	~1	~1	~initial.age.class	~session	Phi(~1)f(~1)p(~1)c(~initial.age.class)f0(~session)	16	3900.8436	70.8744762	0	2201.4522
~1	~1	~sex	~initial.age.class	~session	Phi(~1)f(~1)p(~sex)c(~initial.age.class)f0(~session)	17	3902.79227	72.8231425	0	2201.3427
~1	~1	~citizen + initial.age.class	~session	~session	Phi(~1)f(~1)p(~citizen + initial.age.class)c(~session)f0(~session)	27	3914.73273	84.7636063	0	2192.5075
~1	~1	~citizen	~session	~session	Phi(~1)f(~1)p(~citizen)c(~session)f0(~session)	26	3915.66365	85.6945313	0	2195.532
~1	~1	~citizen + initial.age.class + sex	~session	~session	Phi(~1)f(~1)p(~citizen + initial.age.class + sex)c(~session)f0(~session)	28	3916.6005	86.6313724	0	2192.2781
~1	~1	~citizen + initial.age.class	~session + sex	~session	Phi(~1)f(~1)p(~citizen + initial.age.class)c(~session + sex)f0(~session)	28	3916.656	86.6868724	0	2192.3335

~1	~1	~citizen + sex	~session	~session	Phi(~1)f(~1)p(~citizen + sex)c(~session)f0(~session)	27	3917.22103	87.2519063	0	2194.9958
~1	~1	~citizen	~session + sex	~session	Phi(~1)f(~1)p(~citizen)c(~session + sex)f0(~session)	27	3917.58333	87.6142063	0	2195.358
~1	~1	~citizen + initial.age.class + sex	~session + sex	~session	Phi(~1)f(~1)p(~citizen + initial.age.class + sex)c(~session + sex)f0(~session)	29	3918.52736	88.5582387	0	2192.1041
~1	~1	~citizen + sex	~session + sex	~session	Phi(~1)f(~1)p(~citizen + sex)c(~session + sex)f0(~session)	28	3919.1443	89.1751724	0	2194.8218
~1	~1	~initial.age.class	~session	~session	Phi(~1)f(~1)p(~initial.age.class)c(~session)f0(~session)	26	3930.62745	100.658331	0	2210.4958
~1	~1	~citizen + initial.age.class	~1	~session	Phi(~1)f(~1)p(~citizen + initial.age.class)c(~1)f0(~session)	17	3930.66267	100.693543	0	2229.2131
~1	~1	~citizen	~1	~session	Phi(~1)f(~1)p(~citizen)c(~1)f0(~session)	16	3931.629	101.659876	0	2232.2376
~1	~1	~citizen + initial.age.class + sex	~1	~session	Phi(~1)f(~1)p(~citizen + initial.age.class + sex)c(~1)f0(~session)	18	3932.49503	102.525909	0	2228.9837
~1	~1	~citizen + initial.age.class	~sex	~session	Phi(~1)f(~1)p(~citizen + initial.age.class)c(~sex)f0(~session)	18	3932.53373	102.564609	0	2229.0225
~1	~1	~initial.age.class	~session + sex	~session	Phi(~1)f(~1)p(~initial.age.class)c(~session + sex)f0(~session)	27	3932.54713	102.578006	0	2210.3218
~1	~1	~citizen + sex	~1	~session	Phi(~1)f(~1)p(~citizen + sex)c(~1)f0(~session)	17	3933.15097	103.181843	0	2231.7014
~1	~1	~citizen	~sex	~session	Phi(~1)f(~1)p(~citizen)c(~sex)f0(~session)	17	3933.49657	103.527443	0	2232.047
~1	~1	~citizen + initial.age.class + sex	~sex	~session	Phi(~1)f(~1)p(~citizen + initial.age.class + sex)c(~sex)f0(~session)	19	3934.36961	104.400485	0	2228.7931
~1	~1	~1	~session	~session	Phi(~1)f(~1)p(~1)c(~session)f0(~session)	25	3934.57466	104.605538	0	2216.5329
~1	~1	~citizen + sex	~sex	~session	Phi(~1)f(~1)p(~citizen + sex)c(~sex)f0(~session)	18	3935.02203	105.052909	0	2231.5108

~1	~1	~1	~session + sex	~session	Phi(~1)f(~1)p(~1)c(~session + sex)f0(~session)	26	3936.49065	106.521531	0	2216.359
~1	~1	~sex	~session	~session	Phi(~1)f(~1)p(~sex)c(~session)f0(~session)	26	3936.55515	106.586031	0	2216.4234
~1	~1	~sex	~session + sex	~session	Phi(~1)f(~1)p(~sex)c(~session + sex)f0(~session)	27	3938.47473	108.505606	0	2216.2495
~1	~1	~initial.age.class	~1	~session	Phi(~1)f(~1)p(~initial.age.class)c(~1)f0(~session)	16	3946.5928	116.623676	0	2247.2014
~1	~1	~initial.age.class	~sex	~session	Phi(~1)f(~1)p(~initial.age.class)c(~sex)f0(~session)	17	3948.46037	118.491243	0	2247.0108
~1	~1	~1	~1	~session	Phi(~1)f(~1)p(~1)c(~1)f0(~session)	15	3950.57532	120.606201	0	2253.2385
~1	~1	~1	~sex	~session	Phi(~1)f(~1)p(~1)c(~sex)f0(~session)	16	3952.4394	122.470276	0	2253.0479
~1	~1	~sex	~1	~session	Phi(~1)f(~1)p(~sex)c(~1)f0(~session)	16	3952.5205	122.551376	0	2253.129
~1	~1	~sex	~sex	~session	Phi(~1)f(~1)p(~sex)c(~sex)f0(~session)	17	3954.38807	124.418943	0	2252.9385