









Capybara responses to varying levels of predation risk

Ana Belen Avila ^{a, b, *} , María Jose Corriale ^c , Emiliano Donadio ^{d, 1} ,
 Mario S. Di Bitetti ^{b, a, e} , Marina F. Ponzio ^f, Veronica Cantarelli ^f ,
 Carlos De Angelo ^{a, b, g} 

^a Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Puerto Iguazú, Argentina

^b Asociación Civil Centro de Investigaciones del Bosque Atlántico, Puerto Iguazú, Misiones, Argentina

^c Instituto de Ecología, Genética y Evolución (IEGEB), Universidad Nacional de Buenos Aires (UBA) – CONICET, Capital Federal, Argentina

^d Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIMA), Universidad Nacional del Comahue, CONICET, San Carlos de Bariloche, Río Negro, Argentina

^e Facultad de Ciencias Forestales, UNaM, Eldorado, Argentina

^f Instituto de Investigaciones en Ciencias de la Salud (INICSA-CONICET), Facultad de Ciencias Médicas, Universidad Nacional de Córdoba, Argentina

^g Instituto de Ciencias de la Tierra, Biodiversidad y Ambiente (ICBIA), Universidad Nacional de Río Cuarto (UNRC) – CONICET, Río Cuarto, Córdoba, Argentina

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Predators can generate physiological and behavioural responses in prey individuals. Thus, carnivore reintroductions might cause profound changes in communities and ecosystems by modifying anti-predator responses. Combining observational and experimental approaches, we compared the short- and long-term antipredator responses of capybaras, *Hydrochoerus hydrochaeris*, between a landscape with a high density of predators (Pantanal, Brazil) and a landscape where predators became extinct in the mid-20th century but where a jaguar reintroduction project was in progress (Iberá, Argentina). Generalized linear models were used to test whether the presence of natural predators affects capybara behavioural budgets, gregarious behaviour and the associated physiological stress responses and to test whether, in the short term, capybaras increase their vigilance levels after detecting the proximity of a simulated predator (a playback of jaguar, *Panthera onca*, calls). Capybaras in the Pantanal did not show higher levels of vigilance but they spent a greater proportion of time foraging than did capybaras in Iberá. Pantanal groups were smaller and foraged closer to water. The baseline levels of stress hormones tended to be higher in Iberá. In response to simulated stimuli, both populations responded to predator sound cues by increasing vigilance, but Iberá groups also increased vigilance in response to a control sound, suggesting that they did not recognize the predator stimulus as a greater risk than another stimulus. In areas with predators, capybaras may reduce predation risk by choosing safer areas, where they can spend more time foraging when predators are not nearby. Vigilance may be only a reactive response to cues of the predator's proximity. Understanding the capybara's antipredator responses may help predict the potential effects and the success of jaguar reintroduction in a region where the jaguar has been absent for over 80 years.

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Antipredator responses allow prey to reduce encounters with predators and thus the risk of being killed (Lima, 1998). Carnivore reintroductions might cause profound changes in communities and ecosystems since the presence of predators can generate

physiological and behavioural responses as well as spatiotemporal changes in habitat use of prey (Creel et al., 2008). In this context, the assessment of antipredator responses could provide better predictions of the impact of restored predator–prey interactions.

Antipredator responses can be costly and have deleterious consequences at both individual and population levels (Suraci et al., 2016; Teckentrup et al., 2018). They can decrease the foraging efficiency of prey and their food quality, alter grouping patterns and intraspecific interactions, and can increase stress levels (Preisser & Bolnick, 2008). These responses and their consequences are not necessarily the same in all prey species and environments, and they

* Corresponding author and present address: Instituto de Ciencias de la Tierra, Biodiversidad y Ambiente (ICBIA), Universidad Nacional de Río Cuarto (UNRC) – CONICET, Ruta Nacional 36 Km 601, Río Cuarto (CP 5800), Córdoba, Argentina.

E-mail address: belenavila4@gmail.com (A. B. Avila).

¹ E. Donadio is now at Fundación Rewilding Argentina, Estancia La Ascensión, Los Antiguos, Santa Cruz, Argentina.

may vary according to the predator's hunting mode (Preisser et al., 2007), the prey's ability to perceive risk (Jordan & Ryan, 2015) and to the spatiotemporal distribution of predation risk (Creel et al., 2008), generating different short- and long-term scenarios in which antipredator responses can occur (Creel et al., 2008; Schmitz et al., 2017).

Gregarious herbivores tend to reduce the risk of predation by increasing the time spent vigilant (Creel et al., 2014; Périquet et al., 2010, 2012). Vigilance is a key behaviour because it facilitates the early detection of predators and reduces the likelihood of being killed (Lima & Dill, 1990). However, vigilance can limit the time spent foraging and reduce foraging efficiency (Brown, 1999). Some species reduce the costs associated with vigilance by modifying grouping patterns (Hamilton, 1971), since increasing group size enables increased collective vigilance and reduces the rate of individual vigilance (Lipetz & Bekoff, 1982; Yáber & Herrera, 1994). As a result, high predator areas could cause prey to form larger groups (Thaker et al., 2010).

When an individual faces a predator, the secretion of glucocorticoids (GC), corticosterone or cortisol increases rapidly, mobilizing stored energy, stimulating the immune system and suppressing physiological and behavioural processes that are not immediately essential for survival, such as reproduction and appetite (Sapolsky et al., 2000), improving survival in life-threatening situations (Hawlena & Schmitz, 2010). The physiological consequences of this response will depend on the frequency and duration of predator encounters. Some species have short-term responses to life-threatening situations, decreasing the hormonal response as soon as the stressor disappears, thus avoiding prolonged physiological consequences (Boonstra, 2013; Creel et al., 2009; Wolff & Davis-Born, 1997). Other species respond in the short and long term (chronic stress), generating memory of the attack and thus increasing the ability to anticipate another (Mateo, 2007; Sheriff et al., 2010). However, chronic stress can negatively affect reproductive success and weaken immune function (Boonstra et al., 1998; Cabezas et al., 2007; MacLeod et al., 2018).

These short- and long-term responses to predation risk, both behavioural and hormonal, can combine into different strategies according to the context and the specific prey–predator interaction (Boonstra, 2013). In addition, in environments where the predators have been lost, the time it takes for prey populations to lose antipredator responses is variable, from a few decades to thousands of years (Berger, 1999; Berger et al., 2001), but this is likely a gradual process. The degree to which antipredator behaviours are lost will depend on several factors, including whether previous antipredator behaviours were innate or learned, and on prey generation times (Carthey & Blumstein, 2018). Also, there are different mechanisms to explain the maintenance or loss of antipredator responses, including relaxed selection (Lahti et al., 2009), the multipredator hypothesis (Blumstein, 2006) and naïvety (Carthey & Blumstein, 2014). This variability makes it difficult to extrapolate antipredator strategies between species or predict the consequences of these responses in new situations such as the reintroduction of predators.

We used the capybara, *Hydrochoerus hydrochaeris*, as a model to evaluate whether the presence of natural predators affects antipredator responses. The capybara is a social rodent, native to South America. They are territorial (Herrera & Macdonald, 1989), living in groups of 6–16 individuals (Schaller & Crawshaw, 1981). Adult capybaras weigh 35–70 kg (Ojasti, 1973) and are an important part of the mammal biomass in Neotropical wetlands (Avila, 2017; Desbiez et al., 2010). We evaluated capybara behavioural responses to predation risk and stress levels in two areas that differed in the presence of native top predators: the Brazilian Pantanal (Brazil), where their main predators, jaguars, *Panthera onca*, and pumas,

Puma concolor, are abundant (Azevedo & Murray, 2007; Soisalo & Cavalcanti, 2006), and the Iberá Wetland (Argentina), where pumas are rare and jaguars became extinct 70–80 years ago (Zamboni et al., 2017). For several generations, the herbivores of Iberá have lived in a landscape almost devoid of predation risk. Recently, a jaguar reintroduction project was initiated in this area that might restore predation and its consequences (Zamboni et al., 2017). This underscores the importance of a better understanding of the antipredator responses of the capybara, the main herbivore of this ecosystem.

In this scenario, we compared the antipredator responses of capybaras in these contrasting situations (with and without predators), under the hypothesis that the presence of natural predators affects capybara behavioural budgets, gregarious behaviour and the associated physiological stress responses (Table 1). In addition, we hypothesized that capybaras would increase their vigilance levels after detecting the proximity of a predator; that is, they would show short-term antipredator responses.

METHODS

Study Area

We conducted this study in two wetlands in South America. The Brazilian Pantanal is a 140 000 km² sedimentary floodplain in western Brazil. Annual precipitation is 1000–1400 mm, with seasonally intense rainfall from October to March, followed by a dry season that lasts 3–5 months (ANA, 2005). Mean temperatures range from 32 °C in summer to 21 °C in winter. The Pantanal study site is centred in the Barranco Alto private ranch, located on the shores of the Rio Negro (19°33'34.3"S, 56°10'15.7"W). The landscape presents seasonally flooded savannahs and forest fragments and thousands of permanent small lagoons (Almeida et al., 2011). The main economic activity of the ranch is cattle and ecotourism. Roads are absent in the area, hunting is infrequent and the overall anthropogenic impact on the landscape is considered low (Desbiez et al., 2010). Capybaras live in the ponds and on the edges of the Río Negro, and jaguars and pumas are present (Finnegan et al., 2021), with densities of 6.7 individuals/100 km² reported for jaguars in surrounding areas (Soisalo & Cavalcanti, 2006).

The Iberá region, in northeastern Argentina, is located approximately 1000 km south of the Pantanal study site. Iberá is a 13 000 km² depression located in the ancient course of the Paraná River (Neiff & Poi de Neiff, 2006). Annual rainfall is 1700 mm, with rains concentrated in the warm season (November to March) (Ligier et al., 2004). Mean temperatures range from 28 °C in summer to 16 °C in winter (Neiff & Poi de Neiff, 2006). The Iberá study site is centred in the San Alonso Nature Reserve (28°18'23.2"S, 57°27'15.9"W), a 10459 ha island surrounded by marshes. The landscape is open, with a large area of grassland and interior marshes, ponds and forested patches, with no roads and very little human presence. In 1999, the area became protected, and in 2008, livestock were completely removed from the island. The jaguar is locally extinct, and there have been no records of pumas for at least 10 years prior to the date of the present study, so no predation by big cats has occurred in more than 60 years. Predation on young capybaras occurs occasionally due to the presence of ocelots, *Leopardus pardalis*, feral pigs, *Sus scrofa*, and foxes and caimans (Avila & De Angelo, 2020). Capybaras are more abundant in Iberá than in the Pantanal, with an approximate regional density of 15 individuals/km² in Iberá (Di Giacomo, 2009) and 7 individuals/km² in the Pantanal (Alho & Rondon, 1987; Desbiez et al., 2010). At a local scale, Iberá has high-concentration areas of capybaras, with densities six times higher than at the regional scale (Avila, 2017). Although vegetation composition may differ between sites, both

Table 1

Hypotheses, predictions for response variables, independent variables included in complete models and error structure used for the analysis of capybara's responses to predators

| Hypotheses | Type of response | Prediction (Pantanal relative to Iberá) | Complete model | Error structure |
|--|------------------|---|---|-----------------|
| The presence of natural predators affects capybara behavioural budgets, gregarious behaviour and the associated physiological stress responses | Long term | Group size larger | GS = Site + Group | Conway–Maxwell |
| | | Distance to water shorter | DW = Site | Gaussian |
| | | Proportion of time spent vigilant higher | PtV = Site + DW + GS | Beta |
| | | Proportion of time foraging lower | PtF = Site + DW + GS | Beta |
| | | Proportion of individuals vigilant per group higher | PiV = Site + DW + GS | Binomial |
| | | Proportion of individuals foraging per group lower | PiF = Site + DW + GS | Binomial |
| Capybaras increase their vigilance levels after detecting the proximity of a predator | Short term | Glucocorticoid levels higher | FGC = Site + GS + Group | Gaussian |
| | | Capybaras in the Pantanal will increase the proportion of time spent vigilant after predator stimulus | PtVpost-stimulus = Site*Treatment + PtVpre-stimulus | Beta |

GS = group size; DW = distance to water; PtV = proportion of time vigilant; PtF = proportion of time foraging; PiV = proportion of individuals vigilant; PiF = proportion of individuals foraging; FGC = faecal glucocorticoid concentrations.

areas share a continuous structural gradient from forest to open grassland that is clearly distinguishable, although the configuration and dominance between habitats differs (Di Blanco et al., 2017). Both sites provide refuge for capybara foraging and escape, and cover for stalking of ambush predators.

Behavioural Data Collection

We evaluated 10 groups of capybaras in Iberá and 11 in Pantanal. Observations were conducted in the dry season at both sites, during April–May 2018 in Iberá and July–August 2019 in Pantanal. We recorded group size as the total number of adult, subadult and young individuals (Corriale, 2010).

Behavioural observations were conducted between 1600 and 1900 hours when capybaras commonly prefer to graze on the shore of ponds and lagoons (Corriale, 2010). These observations were made at a distance of 25–100 m from the animals while standing on a 1.5 m ladder. Observations began after the animals showed minimal signs of being disturbed by our presence. If individuals repeatedly directed vigilance towards the observers, the observation was finalized and the data were discarded from the analysis. We randomly selected 10 adult individuals per group and recorded each for 1 min using two Canon SX60 cameras at maximum zoom (62×) (two observers). In groups with <10 individuals, we filmed as many adult individuals as possible (range 4–9). A group scan was also obtained by filming all individuals in the group at the same time to evaluate the proportion of adult individuals performing each activity. During scan sampling, we recorded each individual's distance to water in the group. Each group and each individual were recorded once.

All behavioural recordings were processed to estimate vigilance and foraging budgets for individuals and groups (Altmann, 1974). Individuals were considered foraging when they ingested vegetation and chewed with their heads and ears lowered while standing or lying down. Individuals were vigilant if they looked around attentively, raised their heads above withers height, sniffed in some cases, and held their ears erect. Vigilance was also recorded when individuals were sitting or lying down, looking around attentively, with the chin elevated. Vigilance was classified as social when directed towards conspecifics, and as predator vigilance when animals were clearly scanning the surroundings. Only the latter behaviour was used for the analyses. Because we were unable to identify the sex of all individuals, we conducted an exploratory

analysis with a subset of capybara whose sex could be identified to evaluate the effect of this attribute ($N_{\text{female}} = 80$, $N_{\text{male}} = 61$); we observed no significant effects of sex on the proportion of time spent foraging ($\chi^2_1 = 2.19$, $P = 0.13$), nor on the proportion of time spent vigilant ($\chi^2_1 = 0.49$, $P = 0.47$); thus, all individuals sampled were used in the analyses.

Measurement of Faecal Glucocorticoid Metabolites (FGCM)

Fresh faecal samples were collected in the morning (0800–1000 hours), frozen within 3 h after collection and preserved in a -20°C freezer until analysis. We collected 107 samples from 10 groups in Iberá (April 2018) and 28 samples from four groups in Pantanal (July–August 2019). Groups were visited once, and faecal collection did not overlap with the day on which behavioural observations were recorded. In the laboratory, we extracted corticosterone metabolites (CC) as described by Palme (2005) with slight modifications: 0.5 g (wet weight) of each faecal sample plus 5 ml of 80% methanol in water were incubated in an orbital shaker at room temperature (21°C) for 120 min and finally centrifuged at $\sim 500\text{ g}$ for 20 min. Supernatant containing the steroids was recovered and stored at -20°C . CC concentrations were determined using an enzyme immunoassay (EIA), as previously described (Cantarelli et al., 2017), using polyclonal antibody (anticorticosterone CJM006, C. Munro, University of California, Davis, CA, U.S.A.) and the corresponding horseradish peroxidase conjugate with adjusted dilutions of 1:12 000 and 1:34 000, respectively. FGCM concentrations are expressed as ng/g wet faeces. EIA was performed on serial dilutions of a pool of faecal matter extracts, obtaining displacement curves parallel to the standard curve corresponding to the hormone of interest ($r^2 = 0.98$). In this way, we established that the adequate dilution for CC determination was 1:100. Therefore, before assaying, each sample extract was diluted with phosphate (EIA) buffer (0.1 mM sodium phosphate buffer, pH 7.0, containing 9 g of NaCl and 1 g of BSA per litre) and assayed in duplicate. The sensitivity of the assay was 0.078 ng/ml. The intra- and interassay coefficients of variation were <12% and 5.2%, respectively.

Short-term Behavioural Responses

To evaluate short-term antipredator behaviours of capybaras, we exposed them to sound cues. Five groups of capybaras at each

study site were exposed to predator sounds (jaguar), and five groups were exposed to a control sound (blue macaw, *Anodorhynchus hyacinthinus*). Decibels of both audios were adjusted using the Android application 'Sonometro' (abc Apps). Sounds were reproduced using two external speakers, which were placed 30–50 m from the group. At the time of stimulus experiments, Pantanal groups were, on average, 10 m from water, and Iberá groups were 31 m from water. Both stimulus sounds (predator and blue macaw) were 4 min long, reproduced in blocks of 15 s, 30 s and 45 s and interspersed with 30 s and 60 s periods of silence. For each experiment, the total duration of the stimulus was 10 min. We registered the proportion of time that capybaras spent vigilant and foraging 5 min before and 5 min after exposure to the sound cues (see Behavioural Data Collection above for details).

Ethical Note

We adhered to the ASAB/ABS Guidelines for the ethical treatment of animals in research. We made efforts to minimize disturbance during behavioural data collection by filming from a distance of more than 30 m. The stimuli to which the animals were exposed did not involve manipulation of the animals. The decibels and volume of the sound stimuli were adjusted so as not to generate a greater impact than that of a predator. Faeces collected in the home ranges of the groups did not involve manipulation of the animals.

Statistical Analysis

We evaluated the influence of site (i.e. presence versus absence of large predators) on group size using generalized linear mixed models (GLMM). Since counts of individuals were underdispersed, we used a Conway–Maxwell Poisson error structure and a log link, adding capybara group as a random factor. To evaluate the influence of site on the distance to water, we used the average distance per group as the response variable and we fitted this variable in a linear model (LM). To assess the influence of site on behavioural budgets, we used GLMM. The behavioural budgets for vigilance and foraging were measured as the ratio of the time (seconds) observed per individual displaying each behaviour to the total observation time. These response variables were fitted into two models with a beta error structure and a logit link, with site as the fixed effect and the capybara group as a random factor. As the logit link function of the beta distribution is not defined for the values 0 and 1, we redefined the response variable as $RV' = (RV \times (n - 1) + 0.5)/n$, where RV is the response variable (behavioural budget) and n is the total data set (Smithson & Verkuilen, 2006). Similarly, we evaluated the influence of site location on the proportion of individuals vigilant and foraging using two models with a binomial error and a logit link. In all these models, we added group size and distance to water as covariates. To assess the influence of predator presence on the physiological response (FGCM concentrations), we used linear mixed effect models (LMM). In this model, we added group size as covariate and used capybara group as a random factor. To analyse the effect of natural predator presence on the short-term behavioural budgets, we evaluated the effect of the interaction of the sites with the type of sound cues (jaguar versus macaw) on the proportion of time spent vigilant and foraging after the stimulus. For this purpose, we used a GLMM with a beta error structure, and we included the proportion of time spent performing the pre-stimulus activity as a covariate. Average proportions per group before and after stimulus were used as the response variable.

In all cases, distribution adjustment was assessed graphically from complete model residuals. For models with beta distribution, we used the 'Dharma' package (Hartig, 2020) for assumption validation. We adjusted the binomial model that showed

overdispersion by adding an observation level random effect (OLRE) (Harrison, 2014, 2015). In all analyses, we used a backward selection procedure, removing nonsignificant terms from the model using the likelihood ratio test (Lewis et al., 2011). We used a Tukey test for a posteriori comparison for comparing individual means. We conducted statistical analysis in R v.3.6 (<http://www.r-project.org>) using the packages 'lme4' (Bates et al., 2015), 'glmmTMB' (Brooks et al., 2017) and 'MuMIn' (Barton, 2018). All tests were two-tailed, and differences were considered significant at $P < 0.05$.

RESULTS

Behavioural Responses

Group size and distance to water

Mean group size was smaller in the Pantanal ($\bar{X} = 8$ individuals, 95% CI = [6, 11]) than in Iberá ($\bar{X} = 15$ individuals, 95% CI = [11, 19]; $\beta_{\text{Pantanal}} = -0.55$, $z = -2.67$, $P = 0.005$). Average distance to water per group was greater in Iberá ($\bar{X} = 12$ m, 95% CI = [9, 15]) than in the Pantanal ($\bar{X} = 6$ m, 95% CI = [3, 9]; $\beta_{\text{Pantanal}} = -6.32$, $t = -3.17$, $P = 0.005$).

Vigilance and foraging behaviour

The percentage of time spent vigilant was similar at both sites (Pantanal: $\bar{X} = 13\%$, 95% CI = [10, 17]; Iberá: $\bar{X} = 14\%$, 95% CI = [11, 18]; $\beta_{\text{Pantanal}} = -0.08$, $z = -0.52$, $P = 0.6$). Likewise, the average percentage of individuals that were vigilant per group was very low and similar between sites, not reaching 5% in either of them ($\beta_{\text{Pantanal}} = -1.6$, $z = -1.26$, $P = 0.2$). Distance to water and group size had no influence on the proportion of time spent vigilant (distance to water: $\chi^2_1 = 0.34$, $P = 0.55$; group size: $\chi^2_1 = 0.23$, $P = 0.63$) or on the proportion of individuals performing this activity (group size: $\chi^2_1 = 1.32$, $P = 0.25$; distance to water: $\chi^2_1 = 0.01$, $P = 0.91$).

Baseline foraging behaviours were higher in the Pantanal groups (proportion of time foraging: $\beta_{\text{Pantanal}} = 0.96$, $z = 2.60$, $P = 0.009$; proportion of individuals grazing: $\beta_{\text{Pantanal}} = 1.61$, $z = 2.05$, $P = 0.04$), and in both populations, foraging increased with group size (Fig. 1). Capybaras devoted 60% of their time to this behaviour in the Pantanal (95% CI = [49, 71]) and around 40% of their time to this behaviour in Iberá (95% CI = [26, 50]). The percentage of individuals foraging was 62% in the Pantanal (95% CI = 36, 82) and 25% in Iberá (95% CI = [10, 49]). Distance to water had no influence on the proportion of time spent foraging ($\chi^2_1 = 0.10$, $P = 0.91$) or on the proportion of individuals performing this activity ($\chi^2_1 = 0.004$, $P = 0.94$).

Glucocorticoid levels

Although the FGCM levels were 36% higher in Iberá than in Pantanal (Fig. 2), on average, there was no significant difference between the sites ($\beta = -1151$, $t = -2.10$, $P = 0.054$). Group size had no effect on FGCM levels ($\chi^2_1 = 0.31$, $P = 0.57$).

Short-term behavioural responses

Capybaras spent a higher proportion of time vigilant after a predator stimulus in Pantanal (Table 2, Fig. 3) than in Iberá. Furthermore, capybaras in Pantanal spent a higher proportion of time vigilant after a predator stimulus than after a control stimulus. The Iberá capybaras spent similar proportions of time vigilant regardless of the type of stimulus. Group size and distance to water had no influence on this behavioural response in the experiment (group size: $\chi^2_1 = 0.86$, $P = 0.35$; distance to water: $\chi^2_1 = 0.33$, $P = 0.56$).

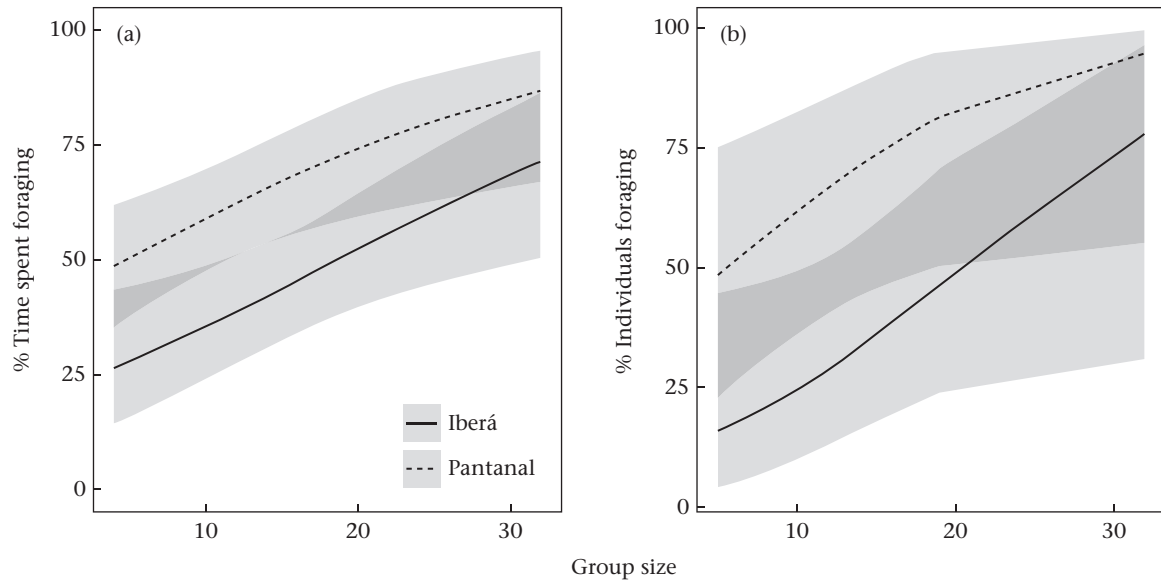


Figure 1. (a) Proportion of time spent foraging and (b) proportion of individuals foraging in relation to group sizes of capybaras living with (Pantanal, Brazil) and without (Iberá, Argentina) large natural predators. The lines correspond to the mean predicted proportion with the 95% confidence interval represented by the grey area.

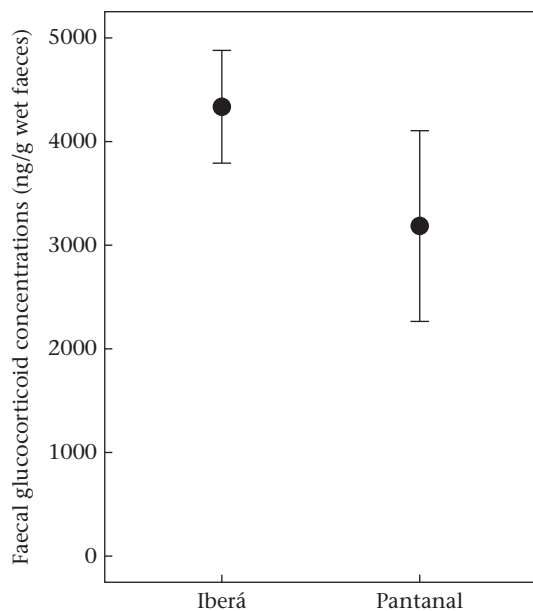


Figure 2. Stress hormone levels (mean \pm 95% CI) predicted by an LMM, in groups of capybaras living in areas with (Pantanal, Brazil; $N = 28$ samples) and without (Iberá, Argentina; $N = 107$ samples) large natural predators.

The proportion of time foraging after the sound stimuli did not vary between the two capybara populations ($\beta_{\text{Pantanal}} = -0.77$, $z = -0.85$, $P = 0.39$).

DISCUSSION

Despite living in an area with a high density of predators, the Pantanal capybaras did not show higher levels of vigilance than the Iberá capybaras that have lived without large predators for decades. However, in the short term, they indeed showed increased vigilance in response to a stimulus. Contrary to our predictions, the Pantanal capybaras spent a greater proportion of time foraging, their groups were smaller and the baseline levels of stress hormones tended to be lower than those of Iberá capybaras. Contrary

to previous observations in this species (Yáber & Herrera, 1994), vigilance rates did not decrease with group size in any of our study areas, but as we predicted, in the Pantanal, these groups were closer to the water than in Iberá. These differences and similarities in antipredator responses of capybaras at both sites provide some important insight into how the process of reintroduction of the jaguar to Iberá could potentially impact capybara behaviours and population dynamics.

Short- and Long-term Behavioural Responses

It is common when comparing antipredator responses between sites to consider only the long-term risk of predation, without considering the temporal variation at each site when interpreting the responses (Creel et al., 2005; Kauffman et al., 2007; Thaker et al., 2011). In our study, the areas were chosen considering the long-term risk of predation, given by the presence and absence of large cats. However, at sites with a high density of predators, such as the Pantanal, there is a short-term temporal variation in the risk of predation, due to the safety and risk pulses associated with the immediate presence of the predator. These short-term changes may explain the differences observed between the two sites.

The interaction between long-term predation risk between sites and short-term temporal variation within each site is described by the predation risk allocation hypothesis (Lima & Bednekoff, 1999). In animals that are frequently exposed to natural predators, the optimal antipredator response to a risk or safety pulse will depend on the context in which the pulse occurs. It suggests that animals spend more time being vigilant and less time foraging during a pulse of risk within a safety context (high-risk situations that are brief and infrequent, such as the predator approaching the area), and they are less vigilant and increase foraging during a safety pulse within a risk context (high density of predators at the site but not in the foraging area). The capybara groups in the Pantanal would thus maintain low vigilance levels and maximize time foraging in moments of greater safety (i.e. when the predator is not nearby) and invest in vigilance when the risk increases due to the imminent presence of the predator, as observed when groups were exposed to predator sounds. In addition, the presence of cattle in an area might cause capybara to increase their foraging time, because

Table 2
Generalized linear mixed model coefficients for the effect of a predator and no-predator sound stimulus on the proportion of time spent vigilant in groups of capybaras living with (Pantanal, Brazil) and without (Iberá, Argentina) large predators, using the time spent vigilant prior to stimuli as covariable

| Selected model | Explanatory variable | Coefficient estimate (\pm SE) | 95% CI | P |
|---|-----------------------------------|----------------------------------|---------------|-------------|
| Site*Treatment + Prop. vigilance pre-stimulus | Intercept | -0.192 \pm 0.718 | -1.599, 1.214 | 0.78 |
| | Site/Pantanal | -1.332 \pm 0.798 | -2.895, 0.231 | 0.09 |
| | Treatment/Predator | -0.282 \pm 0.827 | -1.902, 1.338 | 0.73 |
| | Prop. vigilance pre-stimulus | -3.861 \pm 3.913 | -11.53, 3.808 | 0.32 |
| | Site/Pantanal: Treatment/Predator | 2.217 \pm 1.091 | 0.077, 4.357 | 0.04 |

Shown are means \pm SE, 95% CI and statistical significance (*P*) of the variables included in the model. Significant *P* values are shown in bold.

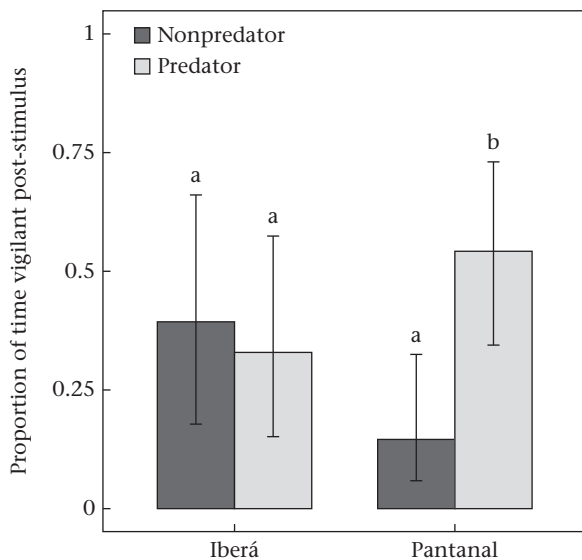


Figure 3. Proportion of time (mean \pm 95% CI) spent vigilant after a predator and a nonpredator stimulus predicted by generalized linear mixed models, in groups of capybaras living with (Pantanal, Brazil) and without (Iberá, Argentina) large natural predators. Different letters indicate statistically significant differences ($P < 0.05$).

cattle may reduce forage availability through trampling and overgrazing (Desbiez et al., 2011; Di Bitetti et al., 2020). In Iberá, the high density of capybara could also reduce forage availability, but as there is no spatiotemporal variation in the risk of predation or in the presence of livestock, the capybaras would not need to compensate for these energy and safety demands.

This pattern of maximized foraging in environments with higher predation when predators are not in close proximity has been observed in other species of herbivores (Périquet et al., 2017; Ylönen et al., 2006) and in studies that compare the strategies of the same species under different risk conditions (Creel et al., 2008). Although increased vigilance is observed most frequently, its relationship with foraging behaviour appears to be variable (Creel et al., 2014; Middleton et al., 2013; Thaker et al., 2011). This variability may be explained by the interaction between the energy compensation that the prey must make when foraging under different short- and long-term risks of predation (Lima & Bednekoff, 1999) and the hunting mode of the main predator (Preisser et al., 2007). In general, the behavioural responses to ambush predators are of greater magnitude than those to active hunters, since ambush predators generate more predictable signals and under more specific landscape conditions, which provides prey with more information to anticipate the threats. Active hunters, on the other hand, generate less predictable signals, having a direct effect on the density of their prey, but without generating major behavioural changes (Luttbeg & Schmitz, 2000). These different effects of hunting mode on prey may explain the differences observed in our study.

In the Pantanal, capybaras are exposed mostly to ambush predators (pumas and jaguars). Low vigilance levels in the Pantanal could be because, in the safety pulses, the capybaras maximize foraging, since they select areas within their home range that they consider to be less risky for this activity. This response is described by the risky place hypothesis (Creel et al., 2008), which predicts that prey avoid areas where the risk of predation is consistently perceived as high. Therefore, the groups of capybaras in the Pantanal, exposed to a prolonged risk of predation, would compensate for the strong behavioural responses that the ambush predator may generate by using safe areas for foraging, and within these areas they assign efforts to vigilance or foraging according to the temporal variation of predation risk. Within their home ranges, the perception of risk could vary spatially, as has been observed in other species (Laundré, 2010; Laundré et al., 2010). In the afternoon hours, the capybaras select areas near the water to feed (Corriale, 2010). These zones may be perceived as safe, so that, in the absence of signs of the close presence of a predator, individuals prioritize feeding activities and minimize vigilance. In Iberá, the only existing predators are medium-sized active hunters (wild pigs and foxes) that could prey upon the young capybaras. Therefore, the absence of behavioural responses in both vigilance and foraging behaviour could be due to capybaras not being exposed to risk and safe pulses given the absence of big cats, and to the fact that the hunting strategies of their current predators do not generate cues that capybaras can associate with risk and to which they can respond with antipredator behaviours.

Hormonal Responses

The lower corticosterone concentration in the Pantanal groups contradicts the accumulated evidence on the positive association between the presence of a predator and an increased concentration of this hormone (Boonstra et al., 1998; Cabezas et al., 2007; Clinchy et al., 2013). However, this association is not always present (Boonstra, 2013; Périquet et al., 2017; Ylönen et al., 2006) and it has even been observed that a population subjected to chronic stress may have lower concentrations of this hormone than a nonstressed population (Mateo, 2007). Lower baseline levels in a more stressed population may indicate desensitization of the individuals to the stress event (the physiological response decreases, but the animal does not learn or adapt) or a depletion of the endocrine system (the system is so fatigued that it cannot sustain a long-term response) (Cyr & Romero, 2009). However, as glucocorticoid hormones do not vary solely as a function of perceived predation risk, other factors, such as social instability, levels of intra- or intergroup aggression and population density, may explain why their concentration was higher in the population with larger mean group sizes and higher group density.

Potential Effects of Jaguar Reintroduction

Jaguars have been absent from Iberá for 70–80 years but are currently being reintroduced. Capybaras represent the most

abundant potential prey in Iberá. If the reintroduction of the jaguar succeeds, we expect that they will generate a greater predation risk for capybaras, although this will be spatially variable depending on landscape characteristics, such as the presence of forests and lagoons and the height of the grasslands. Superimposed on this spatial variation, groups of capybaras will be exposed to temporary pulses of risk and safety and, based on the strategies observed in the groups of capybaras studied, we can expect that they will contextually adjust the proportion of time devoted to foraging and vigilance. We foresee that the impact of jaguars on capybaras will follow two phases. In the short term, we will observe a numerical effect, due to the lack of recognition of predator cues by capybaras, as we observed in our experiments. Capybaras have not been exposed to large carnivores for the last 80 years (a relatively long timeframe according to a capybara generation time of 5.6 years; Pacifici et al., 2013); thus, they are unlikely to respond to these predator cues effectively because they have neither learned about nor adapted to them (Carthey & Blumstein, 2014). The relative naïvety and high density of the Iberá capybaras could forecast a successful jaguar reintroduction in this first phase. In the long term, we expect that with direct and indirect exposure to predators, capybaras will learn to recognize ambush predator cues and reduce the risk of predation through antipredator responses similar to those observed in the capybaras of the Pantanal (Carthey & Blumstein, 2018). The time it will take for capybaras to recognize again the predator's stimuli will depend on their level of naïvety (Banks & Dickman, 2007; Carthey & Blumstein, 2014). Although capybaras in Iberá failed to distinguish between the stimuli of a predator and a nonpredator, they increased vigilance to an unfamiliar stimulus. This could reduce learning times as coexistence with a reintroduced predator would allow specificity to this response (Brown & Chivers, 2005). In addition, changes in the numbers and behavioural patterns of individuals could also generate changes at the ecosystem level, with cascading effects on lower trophic levels (Donadio & Buskirk, 2016; Estes et al., 2011), mainly in the plant communities on which they feed.

Conclusions

Our results suggest that the mere presence of large predators does not necessarily cause an increase in mean levels of vigilance and a decrease in foraging, nor does it necessarily cause an increase in group size and stress hormone levels in capybaras in comparison to populations without predation. The different strategies followed by capybaras in these populations would indicate that, in areas with the presence of predators, capybaras may reduce the risk of being preyed by choosing safer areas, where they can spend more time searching for food when the predator is not nearby, without the need to invest in vigilance. Vigilance could be only a short-term reactive response to an imminent encounter with a predator. However, specific spatial and temporal studies are necessary to be able to confirm the use of these strategies in this species and their potential costs, for example, comparing changes in behavioural budgets throughout the day and between areas within the same site with different predation risk. These different situations may soon be present in Iberá as the founding population of jaguars thrives. Our study provides a baseline for monitoring the behavioural and physiological variables of the capybara once jaguars become established in Iberá.

Author Contributions

Ana Belen Avila: Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Funding acquisition. **María Jose Corriale:**

Conceptualization, Methodology, Writing – Review & Editing. **Emiliano Donadio:** Conceptualization, Methodology, Writing – Review & Editing, Funding acquisition. **Mario S. Di Bitetti:** Conceptualization, Writing – Review & Editing. **Marina F. Ponzio:** Writing – Review & Editing, Formal analysis. **Veronica Cantarelli:** Writing – Review & Editing, Formal analysis. **Carlos De Angelo:** Conceptualization, Methodology, Writing – Original Draft, Writing – Review & Editing, Funding acquisition, Project administration.

Conflict of Interest

We have no conflicts of interest to declare.

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