



RESEARCH ARTICLE - ANTS

New Records and Potential Distribution of the Ant *Gracilidris pombero* Wild & Cuzzo (Hymenoptera: Formicidae)

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Abstract

Gracilidris pombero Wild & Cuzzo, 2006 is an ant that remains poorly studied. Endemic from South America, its geographical distribution is known from few and scattered collection points. In this study, we present new occurrence records of *G. pombero* obtained through extensive collections along the Cerrado biome and the Atlantic Forest of northeastern Brazil. Based on the new and existing occurrence records we produced a model of the geographic distribution of *G. pombero*. Modelling method was chosen based on maximization of model performance after evaluating a series of modelling approaches, including different parametrizations of the Maxent algorithm and distinct runs of the GARP algorithm. We found a total of 43 new records of *G. pombero* in Brazil, including the first records of this species in the states of Goiás, Mato Grosso do Sul, Piauí, Sergipe and Tocantins. Based on our model, the areas of highest suitability of occurrence of *G. pombero* are located in two main zones in South America: one ranging from midwestern Brazil to southeastern Bolivia and Paraguay; and the other spanning the south of Brazil and Uruguay.

Introduction

Gracilidris pombero Wild & Cuzzo, 2006 is the only extant species of the Dolichoderinae ant genus *Gracilidris* Wild & Cuzzo, 2006. The natural history of this species is poorly known but previous studies indicate that colonies are relatively small (Wild & Cuzzo, 2006). This ant builds its nest in the ground, and foraging is predominantly or strictly nocturnal, which may explain why *G. pombero* is poorly represented in entomological collections (Wild & Cuzzo, 2006).

The species was described based on workers collected in a few localities in Paraguay, Argentina and the central and northeastern regions of Brazil (Wild & Cuzzo, 2006; Guerrero & Sanabria, 2011). More recently, *G. pombero*

was found in the extreme south of Brazil, extending its previous known latitudinal range by about 450 km to the south (Feitosa et al., 2015). *Gracilidris pombero* seems to be associated with relatively dry and open habitats, such as grasslands and savannas (Wild & Cuzzo, 2006; Feitosa et al., 2015). However, populations of this species have also been found in the Colombian Amazon and in the Atlantic Forest of northeastern Brazil. Nevertheless, in both cases, the ants were not found in forest areas, but rather in human-managed habitats (such as cattle pastures or cocoa plantations) (Wild & Cuzzo, 2006; Guerrero & Sanabria, 2011).

Based on the known distribution of the living species (*G. pombero*), and a fossil from the Dominican amber [*Gracilidris humiloides* (Wilson, 1985)], Guerrero &



Sanabria (2011) proposed that during drier periods of the Pleistocene *Gracilidris* occurred from Paraguay to Puerto Rico (including the Amazon), but as the climate became wet again during the Holocene, its distribution retracted, resulting in the isolation of populations in the Colombian Amazon. The same hypothesis may also explain the occurrence of *G. pombero* in the Brazilian Atlantic Forest biome. Assuming that *G. pombero* was once much more widely distributed, it is more likely that the Atlantic Forest populations represent relictual populations rather than populations that recently expanded into that region as the result of land cover and land use changes (Guerrero & Sanabria, 2011).

In this study, we present new occurrence records of *G. pombero* obtained through extensive collections of ground-dwelling ants along the Cerrado biome (South American savanna) of central Brazil and along the Atlantic Forest of northeastern Brazil. Based on the new and published information we produced a model of the potential geographic distribution of *G. pombero* in order to identify areas where new discoveries are more likely, and to determine the main climatic variables that help to explain the current distribution of the species.

Materials and methods

Occurrence records

Part of the new records of *G. pombero* presented here come from standardized sampling of the ant fauna conducted in 29 well-preserved savanna sites using pitfall traps (Vasconcelos et al., 2018). These sites were distributed across the entire extension of the Brazilian Cerrado biome, in a region spanning ca. 20° of latitude and 18° of longitude (Vasconcelos et al., 2018).

Records recently published (Santos et al., 2017) obtained from ant surveys performed in several landscapes in the Atlantic Forest biome of the state of Bahia, Brazil, were also included in our analysis. In addition, we examined material deposited in the collection of the Laboratório de Mirmecologia in the Centro de Pesquisa do Cacau – CEPEC/CEPLAC (CPDC) (Ilhéus, Bahia, Brazil), and which include specimens collected in the Cerrado and Pampas biomes, cocoa plantations, or urban areas. Finally, we compiled all published records of occurrence of *G. pombero* through a detailed survey of the literature (Wild & Cuzzo, 2006; Guerro & Sanabria, 2011; Brandão et al., 2011; Neves et al., 2013; Costa-Milanez et al., 2014; Camacho & Vasconcelos, 2015; Feitosa et al., 2015; Meurer et al., 2015; Solar et al., 2016).

Ecological niche modeling (ENM)

The distribution probability map of *G. pombero* was obtained by applying a filtered data set of the occurrence points on several bioclimatic variable layers from the WorldClim database (Hijmans et al., 2005). The modelling method was chosen based on maximization of model performance. This was done after evaluating a series of modelling approaches,

including different parametrizations of the Maxent algorithm (using Maxent software version 3.4.1) and distinct runs of the Genetic Algorithm for Rule Set Production (GARP) (available in the openModeller software v1.1.0; Muñoz et al., 2009). We chose to work with the Maxent and GARP algorithms due to their superior ability and better performance even with a small data set in comparison with other modelling methods (Wisiz et al., 2008). These algorithms have shown success to modeling distributions of several species using occurrence records and environmental data (Peterson et al., 1999; Anderson et al., 2003; Raimundo et al., 2007; Zhang et al., 2015). Additionally, we used the AUC (Average Area under Curve) and sensitivity values to test the performance of our models. Both AUC and sensitivity values ranges from 0 to 1, where a score higher than 0.9 can be considered good predictors of favorable conditions for the occurrence of a species (Phillips et al., 2006).

Data filtering of the 57 available occurrences (see Table 1) was necessary to avoid biased probability estimations (Kramer-Schadt et al., 2013; Boria et al., 2014), since it was observed a spatial aggregation pattern along the map, as a result of intense sampling efforts within some specific regions. Filtering criteria was based on distance between points: for a given group of neighboring occurrences whose distance between one another was less than 2 km, only the central point was maintained. Hence, the filtered data set consisted of 33 occurrence points, which were divided into calibration (27) and validation (6) in order to allow an independent and robust validation. The calibration data were used as the only occurrences available to perform the modeling process, whereas the validation data were considered for validation purposes only.

In order to obtain a consistent model, we evaluated the degree of correlation between the bioclimatic variables based on Principal Component Analysis (PCA), using the software PAST v3.02 (Hammer et al., 2001) as performed by Menezes et al. (2017). Thus, we extracted values of each occurrence point associated to each of the 19 bioclimatic layers using Quantum-GIS v2.8 (Open Source Geospatial Foundation Project, Beaverton, OR, USA) and we checked auto-correlated variables by PCA. Simultaneously, we verified the percent of contribution of each bioclimatic layer and we excluded some non-contributing variables. Finally, from the 19 bioclimatic variables available, only 16 were passed into model algorithms either because of high correlation or due to absence of contribution for our species distribution modelling.

The 27 occurrence calibration points and the 16 bioclimatic variables were passed to several maxent and GARP algorithms, with different parameters. The resultant simulated distributions consisted of two Maxent distributions surfaces and three probability distributions from GARP. The best model was chosen based on the maximization of calibration and validation sensitivity values. Validation was performed by calculating the percentage of validation points located in high probability areas. The final model consisted

of Maxent algorithm run with the following parameters: quadratic, product, threshold and hinge, 500 iterations, regularization multiplier equal 1, thirty percent of random test and ten replicates subsampled. All modelling procedures were developed for the Neotropical Region at a spatial resolution of 2.5°.

Results

New occurrence records

We found 43 new records of *G. pombero* for Brazil, including the first records of this species for the states of Goiás, Mato Grosso do Sul, Piauí, Sergipe and Tocantins (Table 1). Nevertheless, most of the new records were largely coincident or complementary to the previous known range of *G. pombero* in South America. Among the new records, most (70%) were obtained in typical Cerrado vegetation (savanna-like vegetation), 18.5% in agricultural systems (cocoa plantations and small-scale agriculture) or pastures, 7% in the Atlantic Forest biome (fragments with low forest cover and in its surrounding matrix in some cases), 2.3% in urban areas (e.g., university campus), and 2.3% in an abandoned mining area in the south of Brazil (see Table 1).

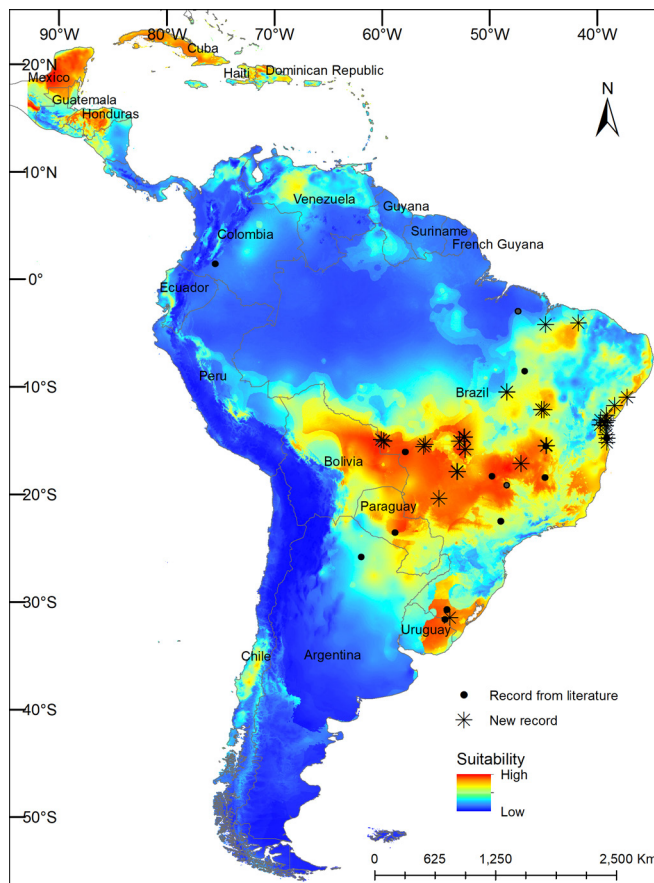


Fig 1. Potential geographical distribution of *Gracilidris pombero* in the Neotropical Region. The intensity of color gradient from blue to red (the redder color means the higher probability of occurrence) is proportional to probability of occurrence.

ENM using Maxent

The performance analysis of the geographic distribution for *G. pombero*, obtained through the best-fit Maxent model, showed high accuracy values, as demonstrated by both AUC and sensitivity metrics. AUC values ranged from 0.92 for calibration dataset and 0.88 for validation data, while sensitivity varied from 0.85 for the calibration and 0.83 considering validation. The small variation observed between calibration and validation performance metrics shows model's ability to predict with high accuracy even in areas in which occurrence points were not available for model fitting, indicating a high degree of confidence on the predicted distribution.

The areas of highest suitability for the occurrence of *G. pombero* were located in two main zones in South America: one ranging from midwestern Brazil to southeastern Bolivia and Paraguay; and the other spanning the south of Brazil and Uruguay (Fig 1). Among these places, for Uruguay and Bolivia have not been registered any occurrence of the species yet. Other suitable regions include the coast of Northeastern Brazil. Moreover, the model predicted high suitability for the occurrence of *G. pombero* also in Central America, notably in the south of Mexico, Cuba, Honduras, and the Dominican Republic, indicating that the entire region has climatic conditions suitable for the species.

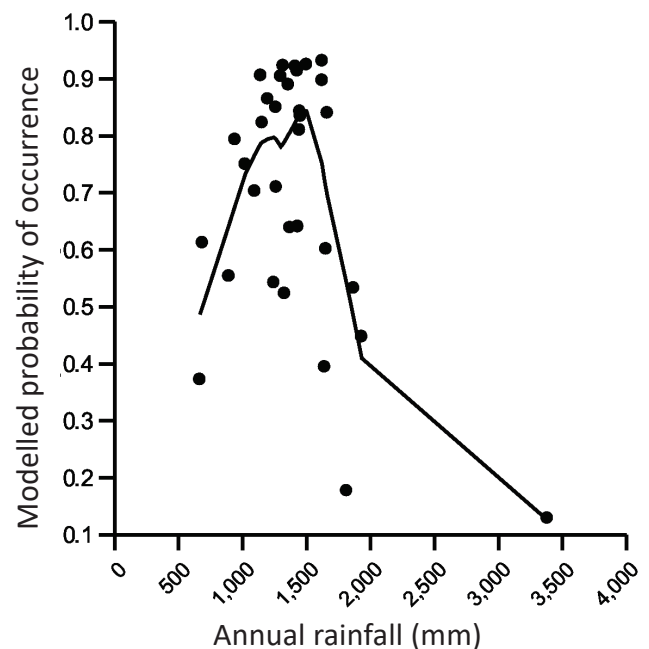


Fig 2. Modelled probability of occurrence of *Gracilidris pombero* in relation to annual rainfall. The line represents a scatterplot smoothing of the data.

Suitable areas were mainly guided by three variables in the model, which alone explained 83% of model prediction: annual precipitation (42.6%), mean temperature of driest quarter (21.4%), and temperature seasonality (18.8%). Furthermore, the model indicates that sites receiving 1,000 to 1,500 mm of rain per year have the highest probability of occurrence of *G. pombero* (see Fig 2).

Discussion

Our study represents a four-fold increase in the number of distributional records of *G. pombero*, from 14 to 57 records. We recorded *G. pombero* in eight Brazilian states, of which five (Goiás, Mato Grosso do Sul, Piauí, Sergipe and Tocantins) have the ant recorded for the first time. Over half of the new records (26 out of 43) were obtained during collections along the Brazilian Cerrado biome and more specifically in cerrado vegetation in biological reserves (Vasconcelos et al., 2018). Most of the remaining records were in eastern Bahia, within the Atlantic forest domain, where it was found in Atlantic Forest fragments of low forest cover and in human-managed habitats, including cattle pastures, cocoa plantations and other small-scale agriculture systems. One record corresponds to an urban area (university campus) in Sergipe. Similarly, the only new record in southern Brazil (Rio Grande do Sul) was in a human-disturbed area (an abandoned mine). These data reinforce the idea that *G. pombero* is a species typical of savannas, shrublands and grasslands, which nevertheless can also be found in disturbed habitats, such as forest edges, pasture, crops and urban areas.

Despite the limited information about the ecology and other specific aspects of the biology of *G. pombero*, we suggest that the large number of new records presented in this study is related to the sampling method used, since most of these records came from pitfall traps (Bestelmeyer et al., 2000), which collect ants with both diurnal and nocturnal habits. *G. pombero* is thought to exhibit nocturnal habits (Wild & Cuzzo, 2006), and this may help to explain the difficulty of collecting it when using other sampling methods, such as visual searches, baits and Winkler traps. It is difficult to find the species even when performing more elaborate soil searches (depths up to 10 cm) if they are carried out during daytime (Guerrero & Sanabria, 2012).

Our distribution modelling suggests that although *G. pombero* has not been collected in Bolivia, it is very likely to be present there. Similarly, there is a strong chance of occurrence of *G. pombero* in northern Uruguay. The areas with highest probability of occurrence of *G. pombero* correspond largely with the distribution of the Cerrado, Chaco, and Pampa biomes of South America. Although *G. pombero* has been recorded several times in the Atlantic Forest, it was always found in relatively open forest sites (three cases; Table 1) or in non-forest habitats, particularly in cocoa plantations and urban areas, reinforcing the view that this species can tolerate some degree of anthropic disturbance (Guerrero & Sanabria, 2011; Feitosa et al., 2015). The expansion of *G. pombero* to areas of this biome may be related to the historic impact of land use change by deforestation, with the replacement of native forests by agriculture or urban centers, intensified principally during the nineteenth and twentieth centuries (Young, 2003) and which continues – at an estimated rate of 29,075 ha deforested per year (SOS Mata Atlântica

and INPE, 2017) – to date. The Brazilian Atlantic Forest currently accounts for about 11.6% of its original vegetative cover (Ribeiro et al., 2009), in a highly fragmented state with more than 80% of these fragments having an area of less than 50 ha (Ribeiro et al., 2011) surrounded by a matrix that can be pasture, agriculture, eucalypt plantations, or urban areas (Joly et al., 2014).

Interestingly, our model indicates a low probability of occurrence of *G. pombero* in the Caatinga, even though this biome is part of the “diagonal of dry biomes”, which also includes the Cerrado and Chaco. In fact, several studies have failed to record this species in the Caatinga (Leal et al., 2003; Ulyssea & Brandrão, 2013; Silva & Delabie, 2014). This biome is drier than the Cerrado and Chaco and, as our model suggests, the probability of occurrence of *G. pombero* declines sharply at relatively dry regions with an annual rainfall of less than 1,000 mm, such as in Caatinga (Ab’Saber, 1993).

Finally, the climatic conditions in Central America seem highly suitable for the occurrence of *G. pombero* although the ant seems totally absent from this region. This finding plus the *Gracilidris* Dominican fossil suggests that the genus *Gracilidris*, in the past, could have occurred both in Central and South America as shown by the known records of the genus (Guerrero & Sanabria, 2011). A similar pattern is suggested for other dolichoderine genera such as *Technomyrmex* and *Bothriomyrmex* with a putative wide geographic distribution in the past but currently restricted to a few isolated forests (Fernandez & Guerrero, 2008). However, further studies exploring the biogeographic history and the divergence time of *Gracilidris* will be necessary to elucidate the geographic origin of the genus.

Acknowledgments

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Table 1. Records of *Gracilidris pombero* in the South America. LT = Literature data; SC = Data of scientific collection (CPDC*); PD = Project data**.

City/locality	State/province	Country	Coordinates		Record type	Habitat type	Reference
			Longitude	Latitude			
Santiago del Estero	Santiago del Estero	Argentina	-61,9113	-25.8547	LT	Chaco	Wild & Cuezco (2006)
Barreiras	Bahia	Brazil	-44,9281	-12,1466	SC	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Barreiras	Bahia	Brazil	-45,1496	-12,1482	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Barreiras	Bahia	Brazil	-45,1382	-12,1446	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Cruz das Almas	Bahia	Brazil	-38,3494	-11,7858	SC	Pasture (cattle pastures)	This study/CPDC
Ilhéus	Bahia	Brazil	-39,1000	-14,7361	LT	Cocoa plantation	Wild & Cuezco (2006)
Ilhéus	Bahia	Brazil	-39,0336	-14,8016	PD	Atlantic Forest (5% coverage); Cocoa plantation	This study/Santos et al., 2018
Inhambupe	Bahia	Brazil	-39,1063	-12,6775	SC	Cocoa plantation	This study/CPDC
Jaguaripe	Bahia	Brazil	-39,0219	-13,1727	PD	Pasture; Small scale agriculture	This study/Santos et al., 2017
Nilo Peçanha	Bahia	Brazil	-39,1961	-13,6488	PD	Pasture; Small scale agriculture	This study/Santos et al., 2017
Pres. Tancredo Neves	Bahia	Brazil	-39,3158	-13,3900	PD	Atlantic Forest (less than 15% of canopy coverage); Cocoa plantation	This study/Santos et al., 2017
Serra Grande	Bahia	Brazil	-39,1000	-14,4833	PD	Cocoa plantation	This study/CPDC
Ubaíra	Bahia	Brazil	-39,6702	-13,1216	PD	Pasture (cattle pastures)	This study/Santos et al., 2017
Una	Bahia	Brazil	-39,0616	-15,1897	PD	Cocoa plantation	This study/CPDC
Valença	Bahia	Brazil	-39,1908	-13,3308	PD	Small scale agriculture	This study/Santos et al., 2017
Wenceslau Guimarães	Bahia	Brazil	-39,7019	-13,5538	PD	Atlantic Forest (less than 40% of canopy coverage); Pasture	This study/Santos et al., 2017
Mineiros	Goiás	Brazil	-53,0085	-17,9088	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Mineiros	Goiás	Brazil	-52,9897	-17,9130	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Mineiros	Goiás	Brazil	-52,9687	-17,9191	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Bacabal	Maranhão	Brazil	-44,7800	-04,2250	SC	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Balsas	Maranhão	Brazil	-46,7178	-08,5721	LT	Cerrado (savanna)	Brandão et al., (2011)
Barra do Garça	Mato Grosso	Brazil	-52,2674	-15,8505	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Barra do Garça	Mato Grosso	Brazil	-52,2540	-15,8573	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Cacéres	Mato Grosso	Brazil	-57,8143	-16,0825	LT	Cerrado (savanna)	Wild & Cuezco (2006)
Chapada dos Guimarães	Mato Grosso	Brazil	-55,9678	-15,3542	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018

Table 1. Records of *Gracilidris pombero* in the South America. LT = Literature data; SC = Data of scientific collection (CPDC*); PD = Project data**. (Continuation)

City/locality	State/province	Country	Coordinates		Record type	Habitat type	Reference
			Longitude	Latitude			
Cuiabá	Mato Grosso	Brazil	-56,1053	-15,5808	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 20188
Nova Xavantina	Mato Grosso	Brazil	-52,3571	-14,7174	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Nova Xavantina	Mato Grosso	Brazil	-52,3116	-14,6969	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Novo São Joaquim	Mato Grosso	Brazil	-52,7876	-15,0785	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Novo São Joaquim	Mato Grosso	Brazil	-52,7798	-15,0695	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Novo São Joaquim	Mato Grosso	Brazil	-52,7773	-15,0592	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Ricardo Franco	Mato Grosso	Brazil	-60,0646	-14,9076	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Vila Bela	Mato Grosso	Brazil	-59,7793	-15,0540	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Vila Bela	Mato Grosso	Brazil	-59,7845	-15,0623	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Vila Bela	Mato Grosso	Brazil	-59,7908	-15,0511	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Campo Grande	Mato Grosso do Sul	Brazil	-54,6857	-20,4228	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Andréquicé	Minas Gerais	Brazil	-44,8475	-18,4524	LT	Wetland areas in Cerrado (“veredas”)	Costa-Milanez et al., (2014)
Pandeiros	Minas Gerais	Brazil	-44,7558	-15,5072	LT	Cerrado (savanna)	Neves et al., (2013)
Pandeiros	Minas Gerais	Brazil	-44,6828	-15,4938	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Pandeiros	Minas Gerais	Brazil	-44,7266	-15,5004	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Paracatu	Minas Gerais	Brazil	-47,0661	-17,1906	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Paracatu	Minas Gerais	Brazil	-47,0583	-17,1790	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Paracatu	Minas Gerais	Brazil	-47,0440	-17,1812	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
São Gonçalo do Abaeté	Minas Gerais	Brazil	-49,7661	-18,3377	LT	Wetland areas in Cerrado (“veredas”)	Costa-Milanez et al., (2014)
Uberlândia	Minas Gerais	Brazil	-48,4000	-19,1666	LT	Cerrado (savanna)	Camacho & Vasconcelos (2015)
Paragominas	Pará	Brazil	-47,3639	-02,9793	LT	Pasture and agricultural areas	Solar et al., (2016)
Sete Cidades	Piauí	Brazil	-41,7095	-4,9910	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Aceguá	Rio Grande do Sul	Brazil	-54,1572	-31,6486	LT	Pampas	Feitosa et al. (2015)
Candiota	Rio Grande do Sul	Brazil	-53,6737	-31,4914	SC	Abandoned mining area	This study
Lavras do Sul	Rio Grande do Sul	Brazil	-53,9813	-30,7005	LT	Pampas	Feitosa et al. (2015)
Agudos	São Paulo	Brazil	-48,9399	-22,4971	LT	Cerrado (savanna)	Feitosa et al. (2015)

Table 1. Records of *Gracilidris pombero* in the South America. LT = Literature data; SC = Data of scientific collection (CPDC*); PD = Project data**. (Continuation)

City/locality	State/province	Country	Coordinates		Record type	Habitat type	Reference
			Longitude	Latitude			
São Cristóvão	Sergipe	Brazil	-37,2050	-11,0029	SC	Public square; University campus (UFSE)	This study
Palmas	Tocantins	Brazil	-48,3512	-10,5264	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Palmas	Tocantins	Brazil	-48,3485	-10,5105	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Palmas	Tocantins	Brazil	-48,3567	-10,5367	PD	Cerrado (savanna)	This study/ Vasconcelos et al., 2018
Florencia	Caquetá	Colômbia	-75,4917	01,4286	LT	Mixed environments highly disturbed by man in the Amazon	Guerro & Sanabria (2011)
Pozo Colorado	Presidente Hayes	Paraguai	-58,7652	-23,5533	LT	<i>Copernicia alba</i> palm forest in the humid chaco	Wild & Cuezso (2006)

*CPDC = Centro de Pesquisas do Cacau, Comissão Executiva do Plano de Lavoura Cacaueira (CEPLAC), Itabuna, Bahia, Brazil; **See acknowledgments section.

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