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Distribution of *Geraeocormobius sylvarum* (Opiliones, Gonyleptidae): Range modeling based on bioclimatic variables

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Abstract. The potential distribution of the harvestman *Geraeocormobius sylvarum* Holmberg 1887 (Opiliones, Gonyleptidae, Gonyleptinae) from Argentina, Brazil and Paraguay, is modeled using the presence-only, GIS-based method Bioclim. The model was run on 2.5 min resolution climate layers using 19 derived bioclimatic variables. The bioclimatic profile of the species is described, and presumable limiting factors in each part of the range are discussed. Modeled distribution of *G. sylvarum* shows a remarkable correspondence to the Alto Paraná Atlantic forest ecoregion, with a marginal presence around the *Araucaria* forests and in gallery/flood forests towards the Southwest. Results support the 650 km yungas-Mesopotamia disjunction, as previously proposed, and reveal that localities in northwestern Argentina have extreme values concerning seasonality parameters with remarkably decreased rainfall in winter. Evidence suggesting that the disjunct pattern may have been derived by antropic introduction is briefly discussed.

Keywords: Neotropics, bioclim, potential distribution, ecological niche modeling, environmental envelope

Harvestmen (Arachnida, Opiliones) are generally regarded as a well suited taxon for biogeographic studies (Ringuelet 1959; Giribet & Kury 2007). Two key features make them useful for those purposes: their low vagility and a close dependence on environmental conditions, mainly humidity (Acosta 2002; Pinto-da-Rocha et al. 2005; Machado et al. 2007). Distribution of most species is thus dependent on the geographic continuity of suitable environments (Acosta 2002). In addition, harvestman endemicity may be particularly remarkable in some areas (Machado et al. 2007). Small-area endemicity is striking in forested ranges like the Brazilian Serra do Mar (Pinto-da-Rocha et al. 2005), and is also important in the montane forests of northwestern Argentina, the so called "yungas" region (Acosta 2002).

However, small-ranged endemics should not be seen as the rule for harvestman distribution. Under certain conditions, many species are known to spread over thousands of km^2 (Curtis & Machado 2007) as long as the suitable environment is not restricted by any geographic or ecological barrier. For example, while many central European species appear geographically restricted, no less than 30 harvestmen in that region extend over quite large ranges (Martens 1978). Broad ranged species are also typical for most of the Argentinean Mesopotamia, which is the humid and sub-humid region between the Paraná and Uruguay rivers (Acosta 2002). Its northernmost portion, roughly matching the administrative province of Misiones, bears subtropical forest physiognomy - actually a part of the "Paranense Biogeographic Province" (Cabrera & Willink 1973) that covers adjacent areas in Paraguay and Brazil as well. The rest of Mesopotamia is a mosaic of shrubs, swamps, grasslands and gallery forests (Hueck & Seibert 1972; Cabrera & Willink 1973). In accordance with these differences, the Mesopotamian opiliofauna has been split into two different, though overlapping, sub-areas (Acosta 2002): the Misiones sub-area and the Mesopotamian *sensu stricto* sub-area. Towards the West, as precipitation decreases, these humid and sub-humid realms give way to the semiarid Chaco, an effective distributional limit for Mesopotamian harvestmen (Acosta 2002).

Geraeocormobius sylvarum Holmberg 1887 (Opiliones, Gonyleptidae, Gonyleptinae) is a large and conspicuous harvestman known to inhabit subtropical forests in northeastern Argentina, southern Brazil and southeastern Paraguay (Ringuelet 1959; Kury 2003; Acosta et al. 2007), being thus characteristic of the Misiones sub-area (Acosta 2002). Acosta et al. (2007) provided several new records for this species; among them three localities in the province of Tucumán, Argentina, revealing a disjunct presence in montane forests in northwestern Argentina (NWA). These separate populations lie about 650 km away from the westernmost record in the core area, with the sub-xeric Chaco in between. As stressed by Acosta et al. (2007), most records of *G. sylvarum* concentrate in the Alto Paraná Atlantic forests ecoregion (referred to as "Paranense forests" below) and in some adjacent sectors of the *Araucaria* moist forest ecoregions (nomenclature after Olson et al. 2001). Argentinean captures outside the mentioned ecoregions (in provinces of Corrientes and Chaco) seemingly are associated with gallery forests and/or seasonal inundation sites (the Humid Chaco and Southern Cone Mesopotamian savanna ecoregions of Olson et al. (2001)). In turn, findings of *G. sylvarum* in NWA correspond to the "tucumano-boliviano" forests, or "yungas" (Hueck & Seibert 1972; Acosta 2002), or the Southern Andean Yungas ecoregion (Olson et al. 2001). The available localities show some spatial bias, since they are concentrated in and around the province of Misiones (a traditionally well sampled area; Ringuelet 1959), while extensive areas in Paraguay are left almost undocumented (cf. Fig. 3).

Interestingly, two further Mesopotamian harvestmen, *Discocyrtus dilatatus* Sørensen 1884 and *D. prospicuus* (Holmberg 1876) (Gonyleptidae, Pachylinae) have Mesopotamia-yungas disjunct ranges as well (Acosta 1995, 2002). A very basic question remains unanswered, however: Are Chacoan conditions really inhospitable to Mesopotamian species or is our record incomplete, leading us to wrongly assume this region to be hostile for harvestmen? Nothing is known about the climatic tolerances of *D. dilatatus*, *D. prospicuus* or *G.*

sylvarum as very little is known about harvestmen physiology and tolerance to physical factors in general (Santos 2007). It is generally accepted that harvestman distribution is governed by climatic constraints, mainly humidity and temperature, but papers addressing how actual climatic conditions affect a given species are almost lacking (Curtis & Machado 2007; Machado et al. 2007).

The occurrence records contain some useful clues. Point records are the very basis for discovering a species range, though the vast majority of Neotropical harvestmen have been scarcely recorded, so that species with more than 15 records are rare (cf. Kury 2003). In fact, most distributional patterns are then intuitively extrapolated from the few records available, emphasizing the need for gathering more data and filling in the gaps. Alternatively, recent developments aimed to model potential species ranges, using available records and several types of environmental predictors, offer innovative methods to help detect areas where presence of a given species may be expected though still not documented (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Hernández et al. 2006; Peterson 2006). Using a Geographic Information System (GIS) and appropriate climate information, the envelope approach infers the species' bioclimatic profile, a species-specific feature (actually, a subset of the fundamental ecological niche) that gives us a rough insight into their presumed tolerance limits, at least with respect to the variables used to build the model. It is then possible to project this profile onto the geographic space, to identify all areas with similar climatic conditions, i.e., where the species would meet a potentially suitable environment (Guisan & Zimmermann 2000; Hijmans & Graham 2006; Hernández et al. 2006; Pearce & Boyce 2006). This paper is intended to characterize the bioclimatic profile of *G. sylvarum* and to model its potential distribution using the BIOCLIM algorithm, taking advantage of the number of records now available for this species (close to the minimum sample size for the method to attain an acceptable accuracy; Hernández et al. 2006). Thereby it is also intended to test if the disjunct Mesopotamian-yungas pattern is supported by the model and to identify areas in which future sampling efforts would be productive in filling in distribution gaps. Results are matched to major biomes and habitat types in order to get a more comprehensive understanding, though still preliminary, of the ecological requirements and potential range of this wide-ranged harvestman.

METHODS

Data acquisition.—All published references for *G. sylvarum* were taken into account (Holmberg 1887; Ringuelet 1959; Soares & Soares 1985; Kury 2003; Acosta et al. 2007). Historical records were inspected for taxonomic reliability (cf. Acosta et al. 2007 for localities excluded), while three localities from the province of Misiones (published by Ringuelet 1959) remained unrecognizable and were set aside: "Campamento Yacu-Poi, near Puerto Bemberg"; "60 km Puerto Iguazú" (which direction?), and "Pasarela Río Uruguay." The full dataset consisted of 48 unique point localities; during the analysis, duplicate records from the same gridcell were removed by the software, resulting in 46 effective records. Localities were identified and geo-referenced using printed road maps and digital gazetteers (mainly NGA GEOnet Names Server [GNS], United States Board on Geographic Names; Google Earth ©), all cross-checked for final accuracy. The label data or collector's information was used to determine location as precisely as possible. Published records typically refer to a locality, which may represent not more than the nearest reference to the actual collecting site; such an imprecision in coordinates (impossible to measure) is deemed not to affect the results considering both the regional scale and coarse approach used.

Climate layers.—The model was run on Worldclim 1.4. (Hijmans et al. 2005a), a set of global climate layers, containing extrapolated monthly data for the 1950–2000 period on maximum, minimum and mean temperature, and precipitation. The 2.5 min resolution (i.e., approximately 4.5 x 4.5 km gridcell) was selected. Information contained in Worldclim (climate data, together with a digital elevation model) is used by the software to derive the 19 bioclimatic variables available for modeling, listed in Table 1. The abbreviation "bc" followed by a number is used below to identify each of these bioclimatic variables.

Modeling method.—Modeling was performed through the presence-only method BIOCLIM, as implemented in Diva-Gis 5.4 (Hijmans et al. 2005b). BIOCLIM is a frequency distribution-based algorithm, which calculates the envelope that bounds the bioclimatic preferences of the species (Fischer et al. 2001; Walther et al. 2004; Hernández et al. 2006). Values of each derived bioclimatic variable are extracted from all localities and arranged in a cumulative frequency distribution (cf. Fig. 2). The envelope is defined as a multi-dimensional hyper-box (each variable representing a dimension) delimiting, at a given percentile, the climatic conditions in the occurrence localities (Guisan & Zimmermann 2000). This set of values constitutes the bioclimatic profile of the species (Fischer et al. 2001), as summarized for the target species in Table 2. In the potential distribution maps (Figs. 1, 4–5), gridcells are scored as suitable (if within the envelope; i.e., the presence of the species can be expected) or unsuitable (outside the envelope). User-defined percentiles were set to define the extent of the envelope (as cut-off) or to rank the gridcells suitability (Fischer et al. 2001; Hijmans et al. 2005b; Hernández et al. 2006).

Evaluation.—The accuracy of the predictive range generated by the model was assessed by calculating the AUC (area under curve) in a receiver operating characteristic (ROC) plot, and the maximum Kappa (max-κ) value, both analyses made in Diva-Gis (Hijmans et al. 2005b). In this study, 70% of the original points were randomly resampled as training data to perform 20 repetitions of the model. Test data included pseudo-absence points selected at random from the background. ROC/max-κ were calculated against the grids stack (0-100 percentile) of the 20 range polygons that were modeled using the training points. AUC values over 0.8 are deemed to reflect a "good" model performance; above 0.9 the accuracy is considered "high" (Luoto et al. 2005). In turn, max-κ over 0.4 are deemed to be "good" and "excellent" if above 0.75 (Randin et al. 2006).

Input variants.—A separate run was performed with records from NWA removed to verify if the species is still predicted in that area. To identify the factors limiting the distribution, the

Table 1.—Median, minimum and maximum values, and range for all 19 bioclimatic variables in the envelope of *Geraeocormobius sylvarum*. Absolute temperature values are in degrees Celsius (° C), precipitation in mm. Numbers preceding each variable are referred to in the text and Table 2. Main differences between profiles with and without yungas records are emphasized in bold.

	All records (n = 46)		Yungas removed (n = 44)	
Bioclimatic variables	Median	Min–max (range)	Median	Min–max (range)
(1) Annual mean temperature	20.39	16.46–23.12 (6.66)	20.62	16.46–23.12 (6.66)
(2) Mean monthly T° range	12.43	10.65–13.83 (3.18)	12.43	10.65–13.83 (3.18)
(3) Isothermality (2/7 x 100)	56.08	47.25–65.00 (17.75)	56.21	49.48–65.00 (15.52)
(4) T° seasonality (STD x 100)	368.87	252.92–**461.59** (208.67)	366.90	252.92–**430.76** (177.84)
(5) Max T° of warmest month	31.65	27.20–34.20 (7.00)	31.70	27.20–34.20 (7.00)
(6) Min T° of coldest month	9.25	4.80–12.50 (7.70)	9.40	4.80–12.50 (7.70)
(7) T° annual range (5–6)	22.50	19.00–25.40 (6.40)	22.45	19.00–24.30 (5.30)
(8) Mean T° wettest quarter	21.52	16.20–25.23 (9.03)	21.36	16.20–25.23 (9.03)
(9) Mean T° driest quarter	16.84	13.40–19.22 (5.82)	16.92	14.03–19.22 (5.18)
(10) Mean T° warmest quarter	24.76	20.33–27.58 (7.25)	24.89	20.33–27.58 (7.25)
(11) Mean T° coldest quarter	16.01	12.35–18.50 (6.15)	16.03	12.50–18.50 (6.00)
(12) Annual precipitation	1723.5	**934**–2235 (1301)	1730.5	**1250**–2235 (985)
(13) Precipitation wettest month	188.5	157–245 (88)	186	157–245 (88)
(14) Precipitation driest month	99.5	**11**–150 (139)	101	**42**–150 (108)
(15) Precipitation seasonality (CV)	20.34	9.42–**83.74** (74.32)	19.94	9.42–**41.88** (32.46)
(16) Precipitation wettest quarter	495.5	432–625 (193)	495.5	432–625 (193)
(17) Precipitation driest quarter	344.5	**40**–496 (456)	349.5	**140**–496 (356)
(18) Precipitation warmest quarter	457	354–625 (271)	455	354–625 (271)
(19) Precipitation coldest quarter	360	**40**–540 (500)	362	**140**–540 (400)

model (full dataset) was alternatively run for each variable separately and combining some of them so as to visually inspect the effects on the resulting predicted range.

RESULTS

Bioclimatic profile.—Table 1 summarizes values relevant to the bioclimatic tolerance range of *G. sylvarum*. Separate profiles with and without the Tucumán localities are given from which it is clear that, for some variables, conditions in the yungas suggest differences from the core area (cf. Table 2 also). Sites from Tucumán represent both the westernmost records and the highest elevation. In those localities precipitation (bc12) is the lowest (Fig. 2B), with rainfall decreasing substantially during the winter (Fig. 2D). There, seasonality is higher than in sites of the core area (Figs. 2A, C); in particular, precipitation seasonality (bc15) is strongly skewed to low values, with both Tucumán records clearly separated by a decided gap from the rest (Fig. 2C). When these localities of NWA are set aside, Rio Tragadero and 10 km Puerto Antequera (close to each other) become the species' westernmost edge and come to hold many of the bioclimatic extremes related to seasonality and winter decrease of precipitation (Table 2 and Fig. 3). However, geographically extreme localities did not necessarily hold the highest or lowest bioclimatic values in all cases (Table 2). Other localities with many bioclimatic variables showing extreme values are Clevelândia (Santa Catarina, Brazil) and Asunción (Paraguay). Clevelândia has nine end values indicating, in general, a cooler and more humid climate than the rest; in turn, Asunción stands as the warmest site of the species range, with highest values for six variables, all temperature-related. With respect to the resulting envelope, a permissive percentile cut-off of 0.005 allowed 33 out of 46 observations (71.7%) to be included within all possible 171 bidimensional envelopes (the remaining 13 observations being outsiders in at least one bidimensional envelope). With the default percentile of 0.025, localities within the species envelope are reduced to 21 out of 46 observations (45.7%).

Potential range.—The predicted range of *G. sylvarum* under the model parameters is displayed in Fig. 1. To a great extent, the predicted core area of *G. sylvarum* roughly matches the Paranense forests ecoregion (Fig. 3). In eastern Paraguay, where records are almost lacking, the prediction partially redraws the boundaries of this ecoregion with the contiguous Humid Chaco (Fig. 3). On the Brazilian side, the predicted range seemingly enters the *Araucaria* forests only marginally, i.e., in areas surrounded by complex eastward Paranense projections that follow large rivers. A large portion of the *Araucaria* ecoregion is scored as unsuitable; moreover, it is to be noted that Clevelândia, one of the localities with many bioclimatic extreme values (Table 2), is placed near this presumable distributional limit (Fig. 3). In Brazil the modeled range reaches up to the southern states of Mato Grosso do Sul and São Paulo in the North (though with no records so far), and weakly up to the western slopes of the Serra do Mar in the East (Fig. 1). *Geraeocormobius sylvarum* was not hitherto collected in the eastern slopes of the Serra do Mar; probably replaced there by its congener *Geraeocormobius rohri* (Mello-Leitão 1933) (A.B. Kury, pers. comm.). On the other side, occurrences of *G. sylvarum* in the northern province of Corrientes and eastern Chaco give support to the potential areas southwest of the paranense forests. Subtropical vegetation partially extends into northern Corrientes, as well as along flood and gallery forests along the Paraná and Paraguay rivers (Hueck & Seibert 1972), and this seems to provide suitable conditions for *G. sylvarum* some hundreds of kilometers away from the main range.

With the full dataset, the bioclimatic model predicts the presence of *G. sylvarum* in the yungas but not across the subxeric Chaco (Fig. 1); thus, the presumed disjunction is

Table 2.—Localities of *Geraeocormobius sylvarum* that represent extreme values, either for geographical coordinates (underlined) or for bioclimatic (bc) variables (numbers as identified in Table 1). Latitude and longitude are given in degrees. Diva-Gis treated the first and second localities as a single point record. In brackets, extreme values of longitude and bc variables if records from Tucumán are removed.

Country	State or Province	Locality	Longitude (W)	Latitude (S)	bc variables, lowest	bc variables, highest	Source
Argentina	Tucumán	Between Cristo and Villa Nougués	−**65.3583**	−26.8083	3, 11	15	Acosta et al. 2007
Argentina	Tucumán	Road to Cerro San Javier, 700 m	−65.3417	−26.8000	3, 11	15	Acosta et al. 2007
Argentina	Tucumán	El Corte (500–700 m)	−65.3333	−26.8083	9, 12, 14, 17, 19	4, 7	Acosta et al. 2007
Argentina	Chaco	Río Tragadero	(−**58.8667**)	−27.4333	(3, 14, 17, 19)	(15)	Acosta et al. 2007
Argentina	Chaco	10 km Puerto Antequera	−58.8000	−27.3833	(14, 17, 19)	–	Acosta et al. 2007
Argentina	Corrientes	Laguna Iberá (Iporá)	−57.1833	−**28.5167**	18	(4)	Ringuelet 1959
Argentina	Misiones	Santa Ana	−55.6000	−27.3667	(12)	–	Holmberg 1887
Argentina	Misiones	Puerto Rico	−55.0333	−26.8000	16	–	Ringuelet 1959
Argentina	Misiones	Salto Encantado	−54.8333	−27.0667	8	–	Acosta et al. 2007
Argentina	Misiones	Piray Miní	−54.6667	−26.3667	–	(7)	Holmberg 1887
Argentina	Misiones	Puerto Bemberg (Pt. Libertad)	−54.6167	−25.9167	–	2 (7)	Ringuelet 1959
Paraguay	Central	Asunción	−57.6333	−25.3000	–	1, 5, 6, 8, 10, 11	Ringuelet 1959
Brazil	Paraná	Clevelândia, Fazenda Tunas	−52.3667	−26.4000	1, 5, 6, 10 (11)	12, 13, 16, 18, 19	Acosta et al. 2007
Brazil	Paraná	Paranavaí	−52.4667	−**23.0833**	13	–	Acosta et al. 2007
Brazil	Paraná	Caviúna, Fazenda Tocantins	−51.3667	−23.3000	4, 7	3	Acosta et al. 2007
Brazil	Paraná	Guaraúna	−50.3667	−25.3333	5 (9)	–	Kury 2003
Brazil	Paraná	Cachoeirinha (nowadays Arapoti)	−**49.8217**	−24.1533	–	–	Soares & Soares 1945
Brazil	Santa Catarina	Nova Teutônia	−52.4000	−27.0500	–	14, 17	Acosta et al. 2007
Brazil	Rio Grande do Sul	Iraí	−53.2500	−27.2000	15	–	Tavares 1980
Brazil	Rio Grande do Sul	São Valentim	−52.5333	−27.5500	2, 7	9	Tavares 1980
Brazil	Rio Grande do Sul	Gaurama	−52.0867	−27.5867	–	9	Acosta et al. 2007

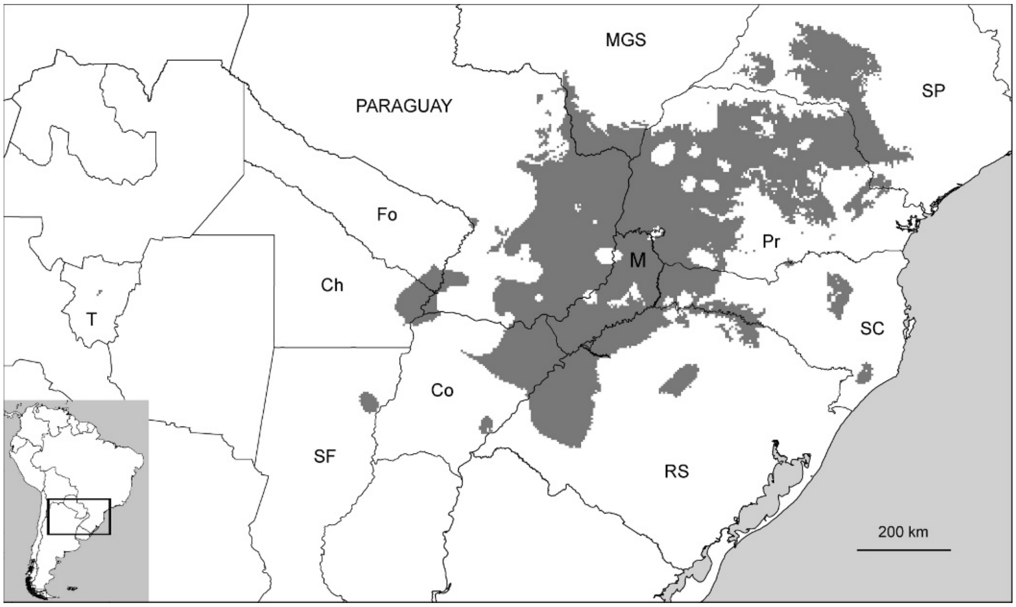

Figure 1.—Predicted range (0-100 percentile) of *Geraeocormobius sylvarum* Holmberg, as modeled with Bioclim, using the full data set and all 19 bioclimatic variables. Provinces in Argentina: T, Tucumán (detailed map in Fig. 4); Fo, Formosa; Ch, Chaco; SF, Santa Fe, Co, Corrientes; M, Misiones. States in Brazil: RS, Rio Grande do Sul, SC, Santa Catarina, Pr, Paraná, SP, São Paulo, MGS, Matto Grosso do Sul.

supported. However, the probability assigned by the model for its occurrence in Tucumán is very low. Even in a 0–100 percentile envelope, suitable gridcells are few (just four), and if ranked, they fit in the lowest percentile levels (Fig. 4A). With a 0.025 cut-off, no suitable gridcell remains in NWA. As expected by these results, modeling with Tucumán records removed did not predict the species there either. Otherwise, modeling the range without these NWA records had minimal

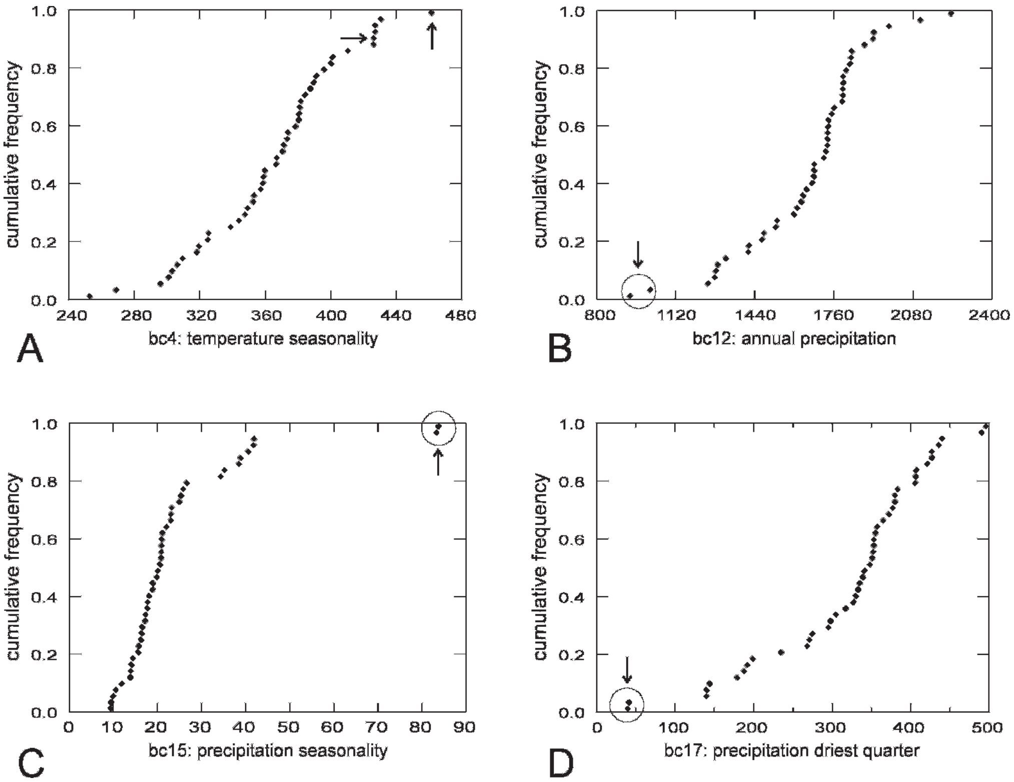

Figure 2.—Bioclimatic profile of *Geraeocormobius sylvarum*, selected variables: full data set plotted for cumulative relative frequency; arrows indicate the position of the two localities from province of Tucumán (NWA). A: bc4 – temperature seasonality (standard deviation x 100); B: bc12 – annual precipitation (mm); C: bc15 – precipitation seasonality (coefficient of variation); D: bc17 – precipitation of the driest quarter (mm).

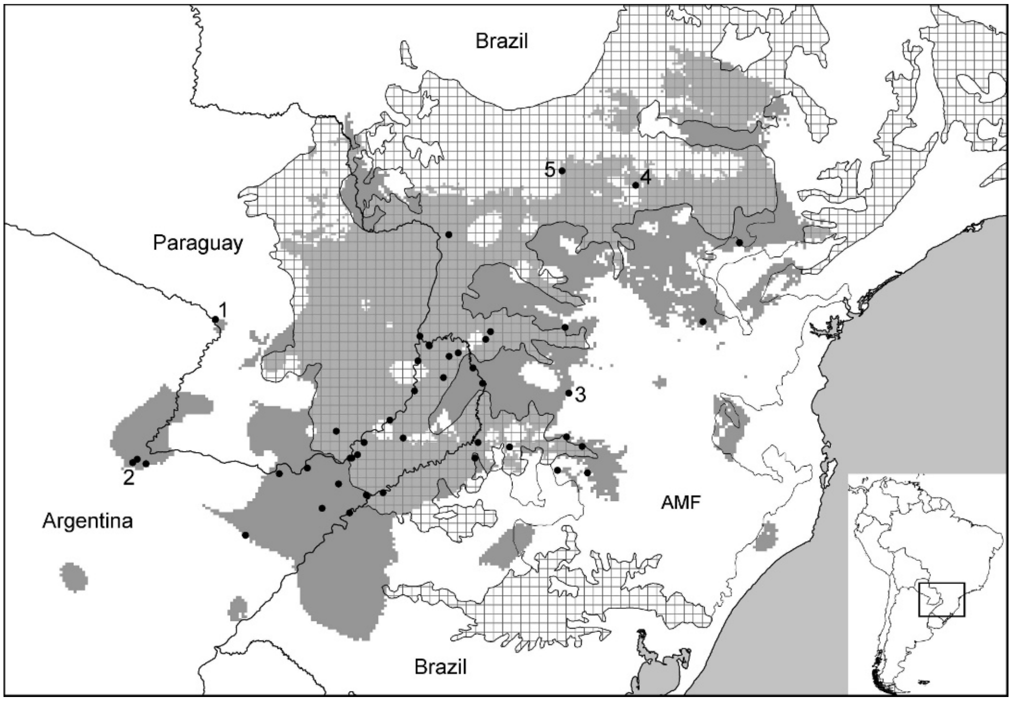

Figure 3.—Correspondence of the modeled range of *Geraeocormobius sylvarum* (grey area, 0–100 percentiles) and the Alto Paraná Atlantic forests ecoregion (squared pattern fill); the overlap is shown as a lighter grey squared area. AMF: *Araucaria* moist forests (bordered by a thin line), where *G. sylvarum* is predicted to occur marginally. Dots: all locality records for the species. References of selected localities: 1: Asunción; 2: Río Tragadero; 3: Clevelândia; 4: Caviúna; 5: Paranavaí.

effects in the core area: just a small clipping occurs, reducing the range on marginal sides, like the Corrientes-Chaco portions, and its northernmost extension in Brazil.

Limiting factors.—Models of *G. sylvarum* run separately, with either temperature (bc1–11) or precipitation (bc12–19) variables, uncover the relative contribution of these variables to the predicted range shape. Prediction based on temperature variables bc1–bc11 (Figs. 4B, 5A) more closely recovers the model obtained by all 19 variables together, with a slight "permissiveness" in the southernmost border (province of Corrientes) and especially in NWA (patchy suitable areas appear along the yungas in Tucumán, Jujuy, Salta, and southern Bolivia). Precipitation variables bc12–bc19 (Figs. 4C, 5B) clip most of these areas away from the model, but, in turn, extend suitable conditions considerably eastwards and northwards. In fact, many precipitation variables (when run alone) predict *G. sylvarum* in the yungas, but almost all prevent it entering the Chaco, some being more rigorous (bc15, bc16, bc18), others more "permissive" (bc12, bc14, bc17, bc19); only bc13 enables a somewhat continuous range. In contrast, only a few temperature variables (bc5 and bc8) contribute to the Chaco gap. Temperature variables are more related to range restrictions in the North and the East. The northernmost boundaries in Brazil, where the range meets the Cerrado and is limited by high temperatures, are fairly well shaped by bc1, bc4, bc6, bc9, and bc11. As noted above, the modeled range

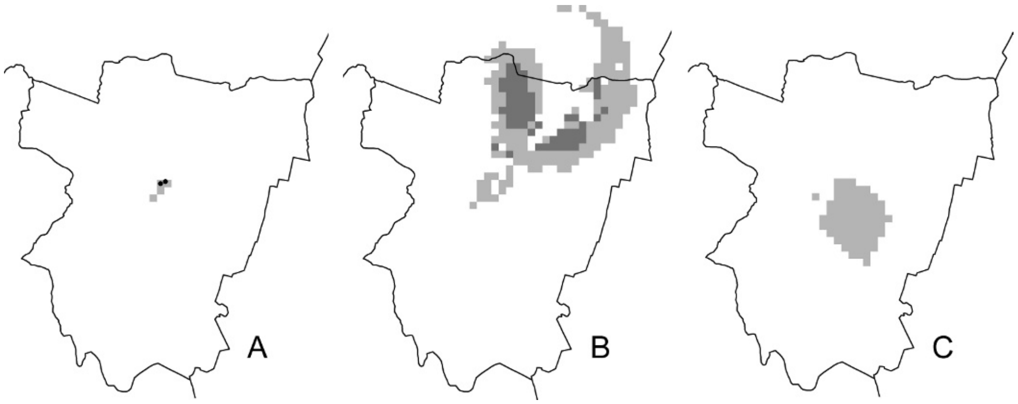

Figure 4.—Detail of the predictive modeling in province of Tucumán, Argentina. A: model with all 19 bioclimatic variables (small dots indicate the occurrence records), B: model with only temperature variables (bc1–bc11), C: model with only precipitation variables (bc12–bc19). Light grey: 0–25 percentile; dark grey: above 0.25.

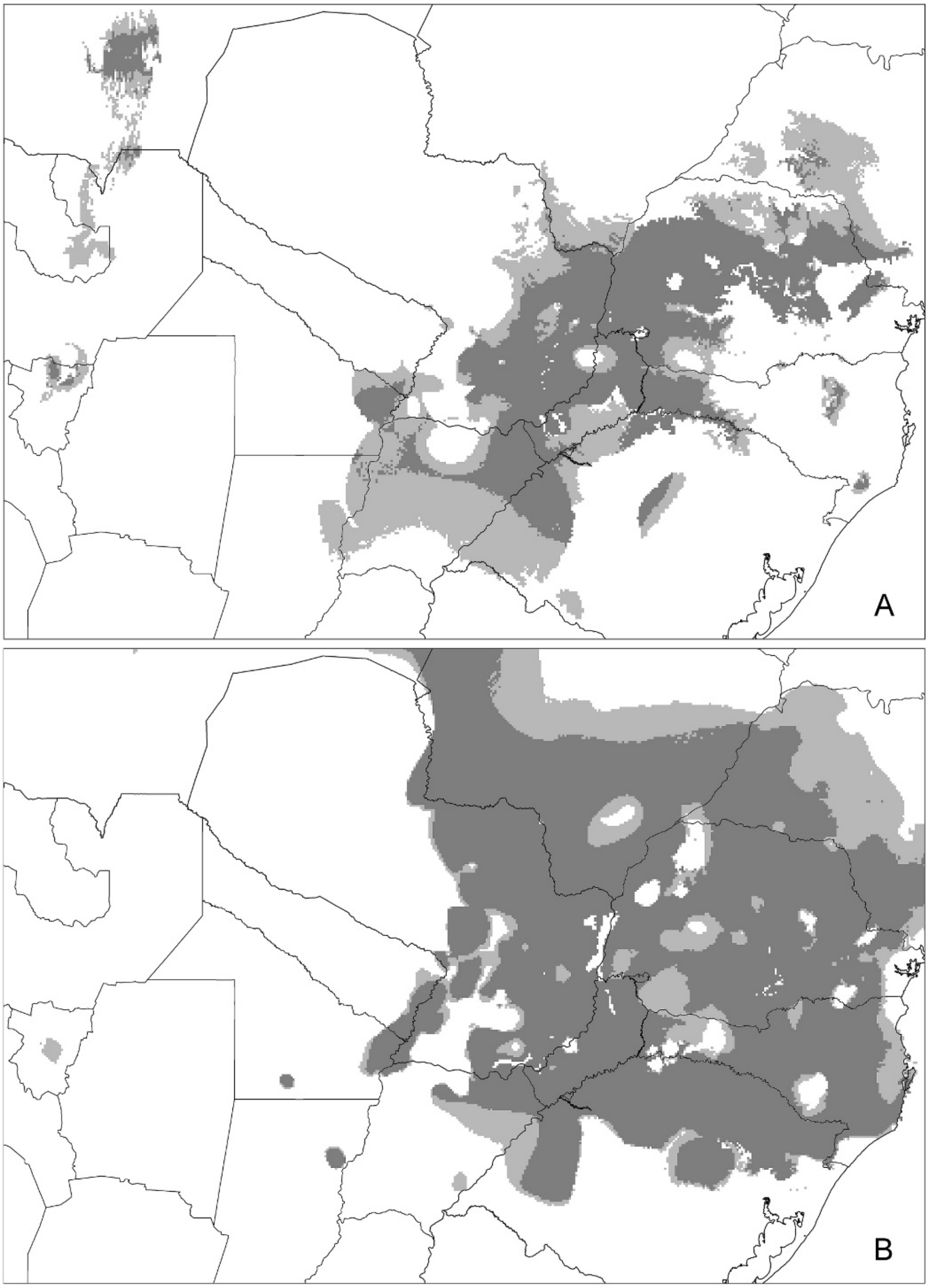

Figure 5.—Potential distribution of *Geraeocormobius sylvarum* modeled only with temperature or precipitation variables (light grey: 0–25 percentile; dark grey: above 0.25). A: modeled range with temperature variables (bc1–bc11), B: modeled range with precipitation variables (bc12–bc19).

seems to circumvent the *Araucaria* forest, entering this ecoregion only marginally (Fig. 3). Several temperature variables (bc1, bc5, bc6, bc8, bc9, bc10, bc11) leave a defined gap there. The unsuitability appears to be related to the high elevation, which in turn causes the seemingly unsuitable cold climate: Clevelândia, elev. 890 m, is the highest record of *G. sylvarum* in Brazil and bears several extreme cold climate values (Table 2), but many negative sites in the *Araucaria* area are above 1100 m.

Accuracy.—Modeling with the training samples (30% of the original points randomly removed) consistently recovered the main portions of the range predicted with all points. More than half of the 20 repetitions matched in most parts of the core area, and just marginal sectors overlapped in only 10 repetitions or less. AUC values ranged from 0.8505 to 0.9402 (mean = 0.8935), and max-κ from 0.7082 to 0.8832 (mean = 0.7900); thus, individual and average AUC and max-κ values resulted in good to high model performances. These values are consistent with performances of Bioclim obtained by Hernández et al. (2006) for similar sample sizes, and with comparative evaluations made by Sangermano & Eastman (2007).

DISCUSSION

As stressed by Peterson (2006), for the vast majority of species nothing more is known than a few "dots on maps" – and certainly, this applies for most Neotropical harvestmen, too. Ecological niche (or habitat suitability) modeling offers a first step towards inferring the basic ecological dimensions that are relevant to limit the species' distribution. While previous knowledge just imprecisely related *G. sylvarum* to Paranense forests (and thereby assumed it was dependent on humid conditions), the bioclimatic analysis provided, for the first time, defined values to describe and discuss the species profile. The envelope method proved to be well suited as an initial approach when species records and biological knowledge are still scarce (Pearce & Boyce 2006). Results were convincing when matching the predicted range polygon to the Paranense forests ecoregion (Fig. 3), a biogeographical area that was previously associated with *G. sylvarum* based on a "non analytical, expert-based" assessment (Acosta et al. 2007). The model accuracy as measured by AUC and max-κ was acceptable as well.

One of the main issues tackled in this paper, the Mesopotamia-yungas disjunction, received support from this model; but at the same time, some new questions arose concerning the presence of *G. sylvarum* in NWA. Despite the availability of presence records, the species is only weakly predicted there. This contrasts with other Mesopotamian harvestmen (*D. dilatatus* and *D. prospicuus* among them) that, in preliminary models, were predicted in the yungas, with or without positive records in NWA (Acosta 2007). Both *D. dilatatus* and *D. prospicuus* belong to the Mesopotamian *sensu stricto* sub-area (Acosta 2002), so their climatic requirements are not expected to be as humidity-dependent as for *G. sylvarum*. Since Bioclim is deemed to over-predict a species' range (Peterson 2001), these facts, together with the profile values for some variables, suggest an important disparity of the bioclimatic conditions of NW and NE Argentina concerning preferences of *G. sylvarum*. However, one should not lose sight of the importance of the resolution of the climatic data. In general the resolution used (2.5 min) is acceptable at a regional scale, but its coarseness may not adequately reflect small-distance variations in montane areas, like in Tucumán (records range from 500 to 1250 m elevation within a distance of less than 3 km; i.e., less than the gridcell size).

As for the causes of the disjunction, a satisfactory explanation remains an open question. Acosta (1995, 2002) suggested that the disjunct ranges of the two *Discocyrtus* species may be a consequence of paleoclimatic cycles, with associated expansion/retraction events affecting the humid forests. A hypothetical vegetational "bridge" (as proposed by Nores 1992 for birds) would have acted as a corridor, enabling Mesopotamian harvestmen to expand their ranges up to the yungas, to leave isolated populations there as climate turned rigorous and the forests retracted. In the case of *G. sylvarum*, however, several elements may render this explanation less likely. Records in the yungas are actually few, indicating a quite limited distribution, and the bioclimatic model accordingly predicts this species only weakly for the region. The yungas is one of the best sampled areas in Argentina for harvestmen (Acosta 2002), so it seems unlikely to find *G. sylvarum* elsewhere in NWA. People from the species' core range are in general aware of *G. sylvarum*, probably because of its large size, abundance and strong odor. These conspicuous and smelly harvestmen are also locally well known in El Corte, although people that have lived there for the last 30 years suggest that the species "appeared" only in recent years (A. M. Frías, pers. comm.). These observations, together with the apparent tolerance of *G. sylvarum* to disturbed areas (Acosta et al. 2007), may suggest that transportation by humans in historic times might best account for the presence of this Mesopotamian harvestman in Tucumán.

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LITERATURE CITED

Acosta, L.E. 1995. Nuevos hallazgos de *Discocyrtus dilatatus* en Argentina, con notas sobre taxonomía, sinonimia y distribución (Opiliones, Gonyleptidae, Pachylinae). Revue Arachnologique 10: 207–217.

Acosta, L.E. 2002. Patrones zoogeográficos de los Opiliones argentinos (Arachnida: Opiliones). Revista Ibérica de Aracnología 6:69–84.

Acosta, L.E. 2007. Distribution of harvestmen (Opiliones) in the Argentinean Mesopotamia: a modeling approach based on bioclimatic variables. 17th International Congress of Arachnology, São Pedro, SP, Brazil. Abstracts. p. 49.

Acosta, L.E., A.B. Kury & M.L. Juárez. 2007. New records of *Geraeocormobius sylvarum* (Arachnida, Opiliones, Gonyleptidae), with a remarkable disjunction in northwestern Argentina. Boletín de la Sociedad Entomológica Aragonesa 41:303–306.

Cabrera, A.L. & A. Willink. 1973. Biogeografía de América Latina. Colección Monografías Científicas O.E.A., serie Biología, n° 13, pp. I–VI, 1–117.

Curtis, D.J. & G. Machado. 2007. Ecology. Pp. 280–308. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Fischer, J., D.B. Lindenmayer, H.A. Nix, J.L. Stein & J.A. Stein. 2001. Climate and animal distribution: a climatic analysis of the Australian marsupial *Trichosurus caninus*. Journal of Biogeography 28:293–304.

Giribet, G. & A.B. Kury. 2007. Phylogeny and biogeography. Pp. 62–87. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Guisan, A. & W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Guisan, A. & N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Hernández, P.A., C.H. Graham, L.L. Master & D.L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773–785.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & A. Jarvis. 2005a. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Hijmans, R.J. & C.H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biology 12:1–10.

Hijmans, R.J., L. Guarino, A. Jarvis, R. O'Brien, P. Mathur, C. Bussink, M. Cruz, I. Barrantes & E. Rojas. 2005b. DIVA-GIS, version 5.4.0.1. Online at http://www.diva-gis.org/

Holmberg, E.L. 1887. Viaje á Misiones. Boletín de la Academia Nacional de Ciencias, Córdoba 10:5–391.

Hueck, K. & P. Seibert. 1972. Vegetationskarte von Südamerika. Vegetationsmonographien der einzelnen Großräumen, 2a: 1–71 + map. G. Fischer, Stuttgart.

Kury, A.B. 2003. Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). Revista Ibérica de Aracnología, Volumen especial monográfico 1:5–337.

Luoto, M., J. Pöyry, R.K. Heikkinen & K. Saarinen. 2005. Uncertainty of bioclimate envelope models based on the geographical distribution of species. Global Ecology and Biogeography 14:575–584.

Machado, G., R. Pinto-da-Rocha & G. Giribet. 2007. What are harvestmen? Pp. 1–13. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Martens, J. 1978. Weberknechte, Opiliones. Die Tierwelt Deutschlands 64:1–464. Gustav Fischer, Jena

Nores, M. 1992. Bird speciation in subtropical South America in relation to forest expansion and retraction. Auk 109:346–357.

Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, J.A. D'Amico, H.E. Strand, J.C. Morrison, C.J. Loucks, T.F. Allnutt, J.F. Lamoreux, T.H. Ricketts, I. Itoua, W.W. Wettengel, Y. Kura, P. Hedao & K. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. BioScience 51:933–938.

Pearce, J.L. & M.S. Boyce. 2006. Modelling distribution and abundance with presence-only data. Journal of Applied Ecology 43:405–412.

Peterson, A.T. 2001. Predicting species' geographic distributions based on ecological niche modeling. Condor 103:599–605.

Peterson, A.T. 2006. Uses and requirements of ecological niche models and related distributional models. Biodiversity Informatics 3:59–72.

Pinto-da-Rocha, R., M.B. da Silva & C. Bragagnolo. 2005. Faunistic similarity and historic biogeography of the harvestmen of southern and southeastern Atlantic Rain Forest of Brazil. Journal of Arachnology 33:290–299.

Randin, C.F., T. Dirnböck, S. Dullinger, N.E. Zimmermann, M. Zappa & A. Guisan. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33:1689–1703.

Ringuelet, R.A. 1959. Los arácnidos argentinos del Orden Opiliones. Revista del Museo Argentino de Ciencias Naturales, Ciencias Zoológicas 5:127–439.

Sangermano, F. & R. Eastman. 2007. Linking GIS and Ecology - The use of Mahalanobis typicalities to model species distribution. Pp. 1–13. *In* Memorias XI Conferencia Iberoamericana de Sistemas de Información Geográfica. (G.D. Buzai, ed.). Buenos Aires.

Santos, F.H. 2007. Ecophysiology. Pp. 473–488. *In* Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Soares, B.A.M. & H.E.M. Soares. 1945. Alguns opiliões do Museu Nacional do Rio de Janeiro. Papéis do Departamento de Zoologia do Estado de São Paulo 5:221–226.

Soares, H.E.M. & B.A.M. Soares. 1985. Contribution à l'étude des opilions (Opiliones: Cosmetidae, Phalangodidae, Gonyleptidae) du Paraguay. Revue Suisse de Zoologie 92:3–18.

Tavares, M.L.R. 1980. Novas ocorrências de opiliões no Rio Grande do Sul e descrição da fêmea de *Melloleitaniana riodariensis* Soares & Soares, 1945 (Arachnida–Opiliones–Gonyleptidae). Iheringia, Série Zoologia 55:155–159.

Walther, B.A., M.S. Wisz & C. Rahbek. 2004. Known and predicted African winter distributions and habitat use of the endangered Basra reed warbler (*Acrocephalus griseldis*) and the near-threatened cinereous bunting (*Emberiza cineracea*). Journal of Ornithology 145:287–299.

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