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Social spiders of the genus *Anelosimus* occur in wetter, more productive environments than non-social species

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Abstract Latitude, rainfall, and productivity have been shown to influence social organisation and level of sociality in arthropods on large geographic scales. Social spiders form permanent group-living societies where they cooperate in brood care, web maintenance, and foraging. Sociality has evolved independently in a number of unrelated spider genera and may reflect convergent evolutionary responses to common environmental drivers. The genus *Anelosimus* contains a third of approximately 25 described permanently social spider species, eight to nine species that all occur in the Americas. To test for environmental correlates of sociality in *Anelosimus* across the Americas, we used logistic regression to detect effects of annual rainfall, productivity, and precipitation seasonality on the relative likelihood of occurrence of social and non-social *Anelosimus* spiders. Our analyses show that social species tend to occur at higher annual rainfall and productivity than non-social species, supporting the hypothesised effects of these environmental variables on the geographical distribution of social species. We did not find support for the hypothesis that permanently social species occur in areas with low precipitation seasonality. High annual precipitation and, to less extent, high productivity favour the occurrence of permanently group-

living *Anelosimus* spiders relative to subsocial and solitary species. These results are partially consistent with previous findings for the Old World spider genus *Stegodyphus*, where a link between high habitat productivity and sociality was also found. Unlike *Anelosimus*, however, *Stegodyphus* typically occur in dry habitats negating a general importance of high precipitation for sociality. Sociality in spiders thus seems to be strongly linked to productivity, probably reflecting the need for relatively high availability of large prey to sustain social colonies.

Keywords Social spiders · Social environment · *Anelosimus* · Distribution range · Precipitation · Productivity

Introduction

Sociality in animals can vary from obligate eusocial living to facultative cooperative breeding. Characteristics of traits such as group size, the number of founding individuals, or the number of reproducers in the group will often vary with environmental conditions (Purcell 2011). Gradients in the degree of sociality have been documented across spatial and environmental clines for a number of animal taxa. Ants, bees, wasps, scorpions, and spiders show latitudinal gradients of their social traits such as colony size and founder numbers, which further vary across several environmental clines. Extensive work on ants has shown that worker size and colony size are largest in temperate latitudes, corresponding to Bergman's clines of increasing body size towards higher latitudes (Kaspari and Vargo 1995; Kaspari 2005). The number of founders of colonies in allodapine bees decreases at lower altitudes (Schwarz et al. 1997), indicating that more benign colony-founding conditions allow for nest foundation by solitary individuals. Facultative solitary halictine bees show intraspecific latitudinal and altitudinal gradients of

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sociality, with social populations found in lower latitudes and altitudes (Plateaux-Quènu et al. 1997; Schwarz et al. 2007; Yanega 1997). Socially polymorphic carpenter bees are more social in areas of heavier parasite pressures, however, without consistent trends coinciding with heavier rainfall (Rehan et al. 2011). All but one of social spider species are predominantly restricted to the tropics and subtropics (Bilde and Lubin 2011), while their less social congeners extend into temperate regions, for example *Anelosimus* (Avilés et al. 2007; Purcell 2011) and *Stegodyphus* (Majer et al. 2013). Intra- and interspecific variation in animal social behaviour across spatial environmental gradients suggest an important role of environmental factors in shaping animal societies.

Social spiders constitute a small minority with approximately 25 of more than 43,000 described extant species (Platnick 2013) scattered across the spider tree of life (Avilés 1997; Kullmann 1972). Social spiders are characterised by permanent group living and cooperation in web building, prey capture, and brood care (Avilés 1997; Lubin and Bilde 2007). The absence of pre-mating dispersal results in regular inbreeding, genetically structured populations, and a female-biased sex ratio (Bilde and Lubin 2011). Phylogenetic analyses indicate as many as 18 independent origins of permanent sociality in six phylogenetically distant genera (Agnarsson et al. 2006a). A unifying pattern for the social species is that they are predominantly tropical and subtropical, with the most species-rich genera occurring in the Americas and Africa (Avilés 1997; Bilde and Lubin 2011). As the only known exception to this pattern, *Anelosimus studiosus* forms multi-female colonies in higher latitudes within its range (Jones et al. 2007). Phylogenetic studies support the conclusion that permanent sociality evolved by elimination of pre-mating dispersal and a transition to intragroup mating and cooperation (Lubin and Bilde 2007), from ancestral species with solitary breeders, extended maternal care, and prolonged communal living among offspring. This periodic social life history also referred to as subsocial behaviour is considered an important first step in the transition to sociality in spiders (Bilde and Lubin 2011; Kullmann 1972). The pattern of multiple origins of sociality that are predominantly restricted to tropical areas suggests that a life history with extended maternal care combined with specific ecological conditions favours the evolution of permanent sociality in spiders.

The spider genus *Anelosimus* contains approximately one third of the permanently group-living species (Agnarsson et al. 2006a). Within this genus, several species throughout the Americas have independently evolved periodic or permanent group living (Agnarsson 2006). Thus, they offer an excellent system to study environmental factors that may influence the evolution of sociality. Most of the permanently social *Anelosimus* species have sister species or clades that are subsocial (Agnarsson et al. 2006a; Avilés 1997; Avilés et al.

2007; Bilde et al. 2005; Lubin and Bilde 2007). Two sister species (*Anelosimus rupununi* and *Anelosimus lorenzo*) are permanently social and thus probably a rare example of speciation within a social spider lineage, while the relationships among the social *Anelosimus eximius*, *Anelosimus domingo*, and *Anelosimus dubiosus* remain contentious. The genus represents a continuum of social behaviours ranging from solitary, such as the vast majority of spiders, to subsocial species with extended maternal care, to permanently social species (Avilés and Harwood 2012). The level of sociality varies both within and among *Anelosimus* species across latitudinal and altitudinal gradients (Avilés et al. 2007; Jones et al. 2007; Purcell 2011; Riechert and Jones 2008). Permanently social species are very rare at high latitudes and at altitudes higher than 1,500 m in the tropics, while subsocial species are rare in tropical lowlands. Within species, median group size in two permanently social species, *A. eximius* and *Anelosimus guacamayos*, decreases with altitude (Avilés et al. 2007; Purcell 2011). These patterns collectively suggest reduced level of sociality with increasing altitude/latitude, which may correlate with decreasing temperature (Pruitt et al. 2012), and productivity.

Variation in the level of cooperation and social characteristics along both latitudinal and altitudinal gradients has been addressed by several hypotheses: rain damage (Avilés et al. 2007; Purcell and Avilés 2008; Riechert 1985; Riechert et al. 1986), ant predation (Purcell and Avilés 2008), and prey size (Avilés et al. 2007; Guevara and Avilés 2007; Purcell and Avilés 2008). The ant predation and rain damage hypotheses attribute the rarity of subsocial species in South American lowlands to decreased survival of females in solitary nests owing to predation by ants or rain damage. The rain damage hypothesis suggests that benefits of permanent group living relative to solitary living should be higher in habitats with more rain due to cooperation in web repairing (Riechert 1985; Riechert et al. 1986) and increased chances of maternal survival in groups with larger, better sheltered nests (Avilés et al. 2007; Riechert 1985).

The prey size hypothesis explains the rarity of permanently social species from South American highlands (Brach 1977; Nentwig 1985) due to a scarcity of large insect prey at high altitudes and thus insufficient prey biomass available to meet the nutritional demand of groups. Insects are the dominant food source of spiders and depend directly or indirectly on primary producers (Borer et al. 2012; Jonsson et al. 2009). As an alternative foraging hypothesis, a constant high prey supply may be an important pre-condition for the evolution of permanent group living. Insect population fluctuations covary with variation in precipitation (Janzen and Schoener 1968; Wolda 1978); hence, the phenology of populations fluctuates more in more seasonal habitats. High variance in prey availability in more seasonal habitats may result in periods of prey abundance that fall below the minimum

required to sustain spider colonies. Accordingly, permanently social species are predicted to occur in less seasonal habitats.

Patterns of altitudinal and latitudinal variation in the social behaviour of species in the genus have been documented at a local scale, such as within same habitats in the tropical rainforests of Ecuador (e.g. Avilés et al. 2007; Guevara and Avilés 2011; Purcell and Avilés 2007, 2008; Purcell et al. 2012) or within species at larger scales (e.g. Jones et al. 2007; Pruitt et al. 2011; Riechert and Jones 2008). However, none of these studies tested for environmental factors which might explain behavioural variation across species at a continental scale. Here we tested for differences in environmental relationships contrasting solitary and subsocial with permanently social *Anelosimus* species across the Americas. We investigated a set of 21 *Anelosimus* species and tested three hypotheses on how environmental factors may determine the relative occurrence of social vs. non-social *Anelosimus*: The *rainfall hypothesis* predicts an increase in the degree of sociality from solitary to permanently social with increasing precipitation (Pruitt et al. 2012). In addition, cooperation in web repair may facilitate foraging opportunities by repairing webs faster, and at a lower cost per individual, after heavy rain. The *productivity hypothesis* assumes that permanently social species should occur in areas of high primary productivity where insects are predicted to be larger (Guevara and Aviles 2007; Nentwig 1985) and more abundant (Majer et al. 2013). In addition, areas of high primary productivity should also hold more structurally complex vegetation that provides more nest sites. For co-occurring species in Ecuador, local-scale differences in habitat use (habitat filtering) due to structural complexity have been demonstrated, such that social species occur in inner forest areas, where the vegetation is sturdier (Purcell et al. 2012). Thus, permanently social species may occur where there are more resources both in terms of food and nest sites. The *seasonality hypothesis* assumes that precipitation seasonality is expected to influence constancy in prey; accordingly, we tested whether permanently social species' habitats are characterised by relatively low precipitation seasonality.

Methods

Study system

The genus *Anelosimus* is cosmopolitan and comprises 63 species (Agnarsson 2006, 2012a; Agnarsson et al. 2010; Platnick 2013). We included 21 species from the Americas in our analysis: ones for which we could obtain occurrence records across their known ranges (Table 1). The hypothesised ancestral behavioural character state in the genus is subsocial (Agnarsson 2006). Avilés et al. (2007) characterised different levels of sociality in *Anelosimus* based on (1) the stage of

Table 1 List of 21 American *Anelosimus* species divided into three groups according to their level of social behaviour on which contrast analysis were performed

Solitary species (3)	Subsocial species (10)	Permanently social species (8)
<i>A. ethicus</i>	<i>A. analyticus</i>	<i>A. domingo</i>
<i>A. nigrescens</i>	<i>A. arizona</i>	<i>A. dubiosus</i>
<i>A. pacificus</i>	<i>A. baeza</i> ^a	<i>A. eximius</i>
	<i>A. chickeringi</i>	<i>A. guacamayos</i>
	<i>A. elegans</i>	<i>A. lorenzo</i>
	<i>A. jabaquara</i> ^a	<i>A. oritoyacu</i>
	<i>A. jucundus</i>	<i>A. puravida</i>
	<i>A. octavius</i>	<i>A. rupununi</i>
	<i>A. studiosus</i> ^a	
	<i>A. tosus</i>	

^a Considered as a separate group of transitionally social species in a complementary analysis (see “Methods” section for further explanation and Appendix 1)

instars when spiderlings or subadults disperse out of the maternal nest, (2) prolonged grouping, and (3) population demography characteristics. We define a social spider as a permanently group-living species where individuals (females) cooperate in breeding and foraging (Aviles 1997; Lubin and Bilde 2007). The overall species list in each behavioural category agrees with (Avilés et al. 2007), but we exclude *Anelosimus jabaquara* from the permanently social group and categorise it as subsocial instead since females perform only limited care for the brood (less complex social behaviour) and the population structure differs slightly from the permanently social species (Marques et al. 1998). Additionally, we consider *A. jabaquara*, *Anelosimus baeza*, and *A. studiosus* as species transitioning from subsocial to permanently social since they form multi-female colonies only in some parts of their ranges.

We gathered all available data on species distributions (Table 1) based on point localities of species records from the published literature, Agnarsson's personal field database, and the GBIF portal (GBIF 2012). All records were mapped and checked for geographic outliers.

Environmental data

For each *Anelosimus* occurrence point, we extracted environmental descriptors from environmental maps in 10' resolution, ca. 5 km² at the equator (Fig. 1). To avoid pseudoreplication, only one of more occurrence points falling within the same cell was used (separately for social and non-social species). We selected the following environmental variables: annual precipitation, the globalised difference vegetation index (GVI), and precipitation seasonality to test

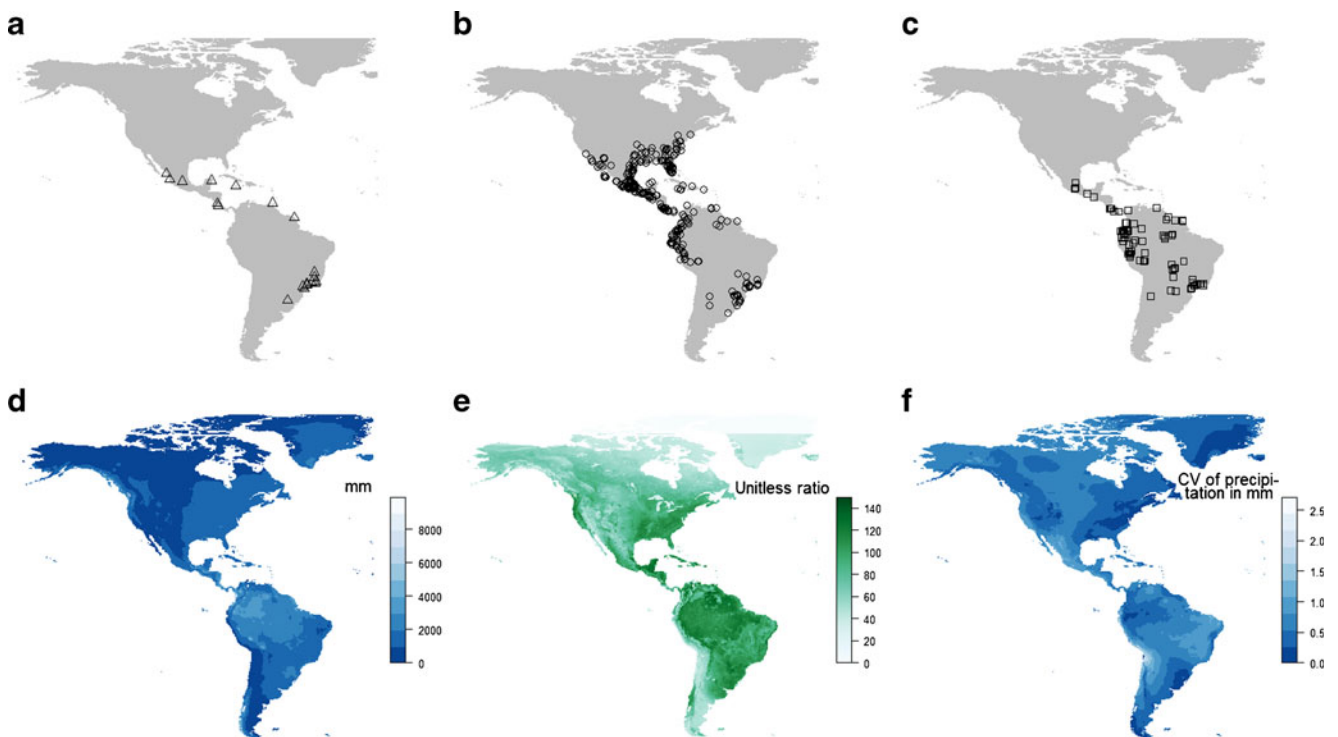


Fig. 1 Distribution maps of the American *Anelosimus* species: three solitary (a), ten subsocial (b), and eight permanently social species (c). Gradients of three environmental variables which we relate to the underlying hypotheses for the distribution of American *Anelosimus*

species are mean annual precipitation (d), vegetation productivity (GVI) (e), and precipitation seasonality (f). The lighter the blue is in (d) and (f), the more rainy and seasonal in rainfall the area is. The darker the green is in (e), the more productive it is

the rainfall, productivity, and seasonality hypotheses, respectively. The climatic variables were obtained from CliMond dataset (Kriticos et al. 2012). Annual precipitation was computed as the sum of monthly average rainfall values in millimetres for 1960–2000. Precipitation seasonality was calculated as a coefficient of variation of the monthly average precipitation values. GVI is a measure of the mean annual normalized difference vegetation index (NDVI), which is the most common remote sensing measurement of vegetation productivity, obtained from the EDIT Geoplatform (Clark Labs 1998). It was derived from satellite images for 1982–2000, with the original NDVI values rescaled to range 0–255 (byte format). A yearly average GVI was computed from NDVI by averaging the monthly means.

Statistical methods

Two sets of logistic regressions were performed to test the three study hypotheses. In each model, the occurrence of social vs. non-social species was contrasted, setting social as 1 and non-social as 0, grouping subsocial and solitary species. It is reasonable to group these as subsocial species spend their entire adult life and part of their juvenile life stages living solitarily. In a subsequent analysis, we excluded solitary species from the analysis as there were only 20 occurrence points for these to test the strength of the pattern. Contrasts

were performed using generalised linear models. The Akaike Information Criterion (AIC) was used to assess support for the various models and the three predictor variables (Johnson and Omland 2004). Akaike weights for each model were furthermore used to derive multi-model coefficient estimates for each predictor. These coefficients were then used to estimate odds of sociality as a function of a given predictor (Franklin 2009).

To account for spatial autocorrelation in our data, we included spatial filters (Diniz-Filho and Bini 2005) as additional predictors in logistic regressions. These are eigenvector-based variables computed on geographical coordinates of data points, which capture the spatial patterns in the dataset from broadest to increasingly finer scales (Diniz-Filho and Bini 2005). The final set of filters included as predictors in the model were chosen by inspecting correlograms of model residuals (Diniz-Filho and Bini 2005). Only filters that were not significantly correlated with environmental predictors were included. Finally, by checking correlograms of residuals from all models including environmental predictors and the selected spatial filters, we checked that only negligible spatial autocorrelation remained in model residuals (non-significant Moran's I values). The generalised R^2 was used as a measure of model explanatory power (Nagelkerke 1991). The statistical modelling was done using SAM (Rangel et al. 2010) and R (R Development Core

Team 2011). Qualitatively similar results were derived from both comparisons.

Results

Annual precipitation and productivity (GVI) had well-supported effects on the relative occurrence of social vs. non-social species (Tables 2 and 3), with social species occurring at higher rainfall and higher vegetation productivity (Figs. 2 and 3). Precipitation seasonality received relatively weak support (Table 2), with a tendency for social species to occur at relatively higher precipitation seasonality than non-social species (Table 3). Thus, no support was found to support the prediction that social species occur in areas with low precipitation seasonality.

Effects of precipitation and productivity were similar when contrasting social vs. subsocial species while excluding solitary species; analyses showed strong support for annual precipitation to predict sociality and weaker support for vegetation productivity as a predictor (Table 3). Finally, results of an additional analysis contrasting social species to three transitionally social species (*A. baeza*, *A. jabaquara*, and *A. studiosus* with occasional multi-female colonies;

Table 2 Performance of logistic regression models predicting social vs. non-social *Anelosimus* species occurrences (93 social/340 non-social, total number of observations=433) across the New World and social vs. subsocial species (93 social/320 subsocial)

Model	Predictors	AIC	∂ AIC	w_i	R^2
Social (1) vs. non-social (0)					
1	PRE _{mean}	336	5.007	0.054	0.280
2	PRE _{seas}	390	58.738	0.000	0.161
3	PRE _{mean} +PRE _{seas}	337	6.111	0.031	0.282
4	GVI	362	30.614	0.000	0.223
5	GVI+PRE _{mean}	333	1.872	0.258	0.292
6	GVI+PRE _{seas}	363	31.812	0.000	0.225
7	GVI+PRE _{mean} +PRE _{seas}	331	0.000	0.657	0.300
Social (1) vs. subsocial (0)					
1	PRE _{mean}	318	3.475	0.108	0.306
2	PRE _{seas}	377	62.959	0.000	0.171
3	PRE _{mean} +PRE _{seas}	317	2.638	0.165	0.313
4	GVI	352	37.845	0.000	0.228
5	GVI+PRE _{mean}	318	3.442	0.110	0.311
6	GVI+PRE _{seas}	353	38.722	0.000	0.231
7	GVI+PRE _{mean} +PRE _{seas}	314	0.000	0.616	0.323

The Akaike scores (AIC), differences (∂ AIC), and weights of each model (w_i) are given. Four spatial filters were included in all the models to account for spatial autocorrelation in the data. In italics are the Akaike weights of the best supported models

GVI globalised difference vegetation index, PRE_{mean} mean annual precipitation, PRE_{seas} precipitation seasonality

Appendix 1) showed that annual precipitation received the strongest support and sociality was predicted in areas with more precipitation (Appendixes 1 and 2).

Discussion

We tested three spatial hypotheses on environmental predictors of sociality in the genus *Anelosimus*, using a comprehensive dataset of the American species ranging in social behaviour from solitary to permanently social. Our results corroborate the two hypotheses linking geographical patterns of sociality in the genus with annual gradients of precipitation and, less strongly, productivity. Annual precipitation as an environmental predictor was well supported and indicated the occurrence of social spiders in areas with heavier rainfall, consistent with the rainfall hypothesis. The productivity hypothesis was moderately well supported and indicated that habitats characterising permanently social species are more productive, which is associated with higher prey abundance. In contrast to our prediction, we found little support for lower precipitation seasonality in social environments. Our results from this analysis on the contrary may even indicate that degree of sociality increases with precipitation seasonality.

Annual precipitation was the most important environmental predictor of permanent sociality when contrasting social to non-social *Anelosimus*. We found permanently social species to occur in areas of higher precipitation, a result that conforms to the rain disturbance and maternal survival hypotheses for permanent group living in the genus. Due to the effect of rain disturbance, larger

Table 3 Multi-model coefficient estimates for all three environmental predictors across the models (Table 2)

Variable	Multi-model β	Odds	Coefficient support
Social vs. non-social			
PRE _{mean}	2.439	11.456	1.000
GVI	1.083	2.955	0.915
PRE _{seas}	0.589	1.802	0.688
Social vs. subsocial			
PRE _{mean}	2.851	17.309	1.000
PRE _{seas}	0.768	2.156	0.781
GVI	0.678	1.969	0.727

Given are the coefficient estimates based on the standardised coefficient and model weights (Multi-model β =Std. β * w_i), the odds of being more social (outcome 1 in all models), and the relative coefficient support in each model set based on the sums of the Akaike weights of the models containing each predictor (Table 2). Social vs. non-social contrasts are models where the social species occurrence points were contrasted to solitary and subsocial species

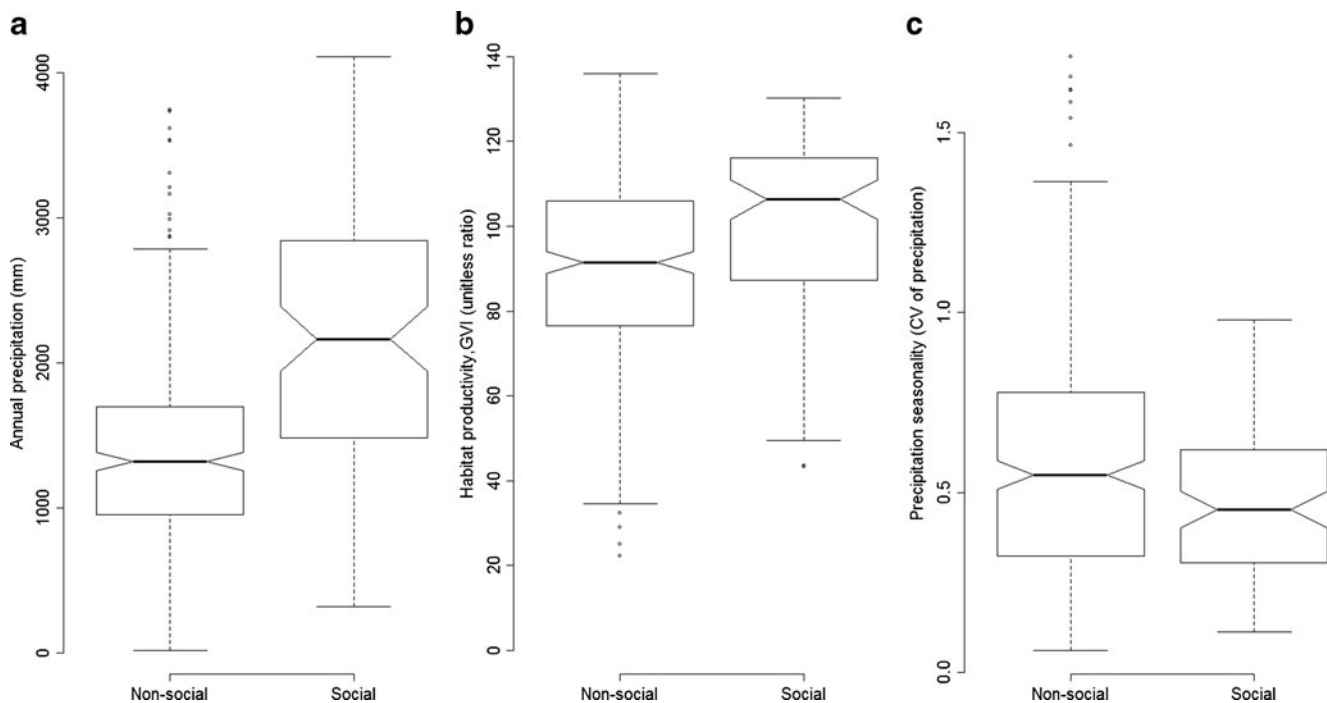


Fig. 2 Boxplots of environmental gradients representing the underlying hypotheses for the distribution patterns of American *Anelosimus* species, for non-social (20 solitary plus 320 subsocial records) and social species locality records (93). The extremes, the interquartile range, and the

median are shown for annual precipitation (**a**), habitat productivity (GVI) (**b**), and precipitation seasonality (**c**). Scales differ for each of the three variables (see “Methods”)

groups should perform better in wetter habitats since their nests are larger and more compact, thus more resistant to rain showers (Avilés et al. 2007). While not explicitly testing the rain damage hypothesis, Pruitt et al. (2012) also found a positive correlation of sociality with annual precipitation in the occurrence of 12 American *Anelosimus* species in single locations. A transplant experiment with subsocial *Anelosimus* showed that females tend to be subject to higher mortality in lowland rainforest areas of South America due to heavy rains, and the average rainfall intensity rather than average daily rainfall per se was associated with better group performance (Purcell and Avilés 2008). A low abundance of subsocial *Anelosimus* in the lowland rainforests may perhaps not reflect their inability to occupy this habitat but rather that subsocial species that come to occupy this habitat rapidly evolve sociality. That sociality may evolve rapidly is evidenced by the socially polymorphic *A. studiosus* in North America (Jones et al. 2007; Pruitt et al. 2008; Riechert and Jones 2008). How frequent such polymorphism is in response to environmental variable in tropical species, however, remains largely unstudied and thus unknown.

The rain disturbance hypothesis was proposed for another social spider living in the African equatorial rainforests, *Agelena consociata* (Riechert 1985; Riechert et al. 1986). With increasing group size, social spiders survived the tropical heavy rains better if they were sheltered in large nests. An

additional benefit for females is to reduce the cost of silk production by joining existing colonies. In other group-living animals, variation in precipitation patterns rather than precipitation per se was proposed to influence the occurrence of cooperative breeders with higher degree of cooperation in more variable environments (Jetz and Rubenstein 2011). In contrast to cooperatively breeding birds, permanently social spiders seem to be more affected by the overall amounts of rainfall. We conclude that precipitation gradients influence the continental distributions of non-social and permanently social species in New World *Anelosimus* with higher degree of sociality in areas of higher precipitation.

A set of studies on *A. studiosus* showed that populations of this species are more social in higher latitudes of North America (Jones et al. 2007; Jones and Riechert 2008; Pruitt et al. 2011; Riechert and Jones 2008). This latitudinal shift in social structure that is opposite to sociality gradients observed in the genus overall was attributed to a type of maternal survival hypothesis. According to the fostering model developed to explain this pattern, solitary *Anelosimus* females have a higher chance of offspring survival in warmer sites (Jones et al. 2007). Multi-female colonies in this species form with higher probability at colder sites; still, solitary breeding is more prominent within those sites (Jones and Riechert 2008). We did not explore the role of temperature on distribution patterns here; however, temperature and primary productivity

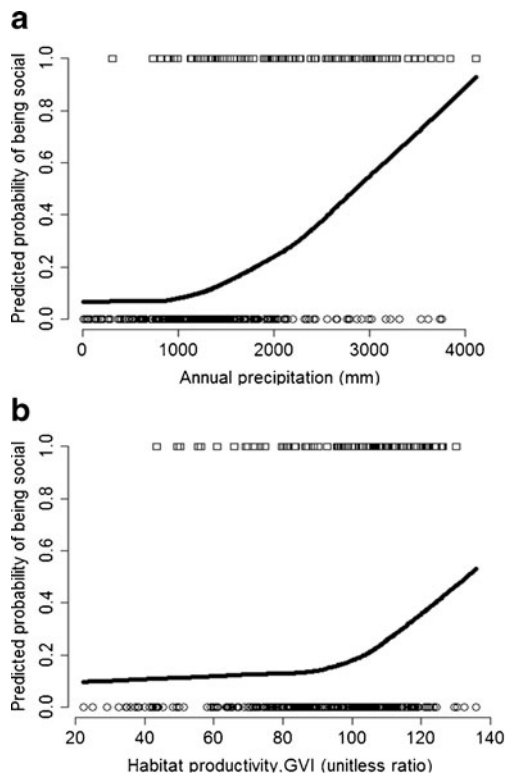


Fig. 3 Predicted probability of sociality on the gradient of annual precipitation (**a**) and habitat productivity (**b**) when contrasting social (empty squares) to non-social (empty circles) *Anelosimus* species. The probability functions were estimated by logistic regression using annual precipitation and spatial filters (**a**) and vegetation productivity and spatial filters (**b**) as predictors (see models in Table 1). The lines indicate response curves estimated by smoothing the probabilities predicted by the precipitation+spatial filters model in (**a**) and vegetation productivity+spatial filters model in (**b**)

correlate strongly across continental scales, and we explored the role of the latter in this study.

The evolution of group living is often driven by foraging benefits (Davies et al. 2012), and both prey abundance (Majer et al. 2013) and prey size (Guevara and Aviles 2007; Nentwig 1985; Powers and Aviles 2007) are proposed as decisive factors for the maintenance of group living in spiders (Aviles 1997; Lubin and Bilde 2007; Whitehouse and Lubin 2005). We examined two hypotheses associated with prey availability, namely productivity and seasonality hypotheses. First, we predicted permanently social species to occur in areas of high productivity, which are associated with high insect biomass abundance (Borer et al. 2012; Clarke and Gaston 2006). Productivity was a well-supported predictor of sociality when contrasting social to non-social species, and social species occurred in more productive habitats.

The positive effect of productivity documented here is consistent with results of a study on species distribution ranges of social and solitary species of the spider genus *Stegodyphus* across the three Old World continents (Majer et al. 2013). In that study, group-living spiders were restricted

to areas with high productivity which correlates with high insect prey biomass, indicating that habitat productivity constrains the distribution of social species. The Old World *Stegodyphus* spiders occupy arid and semi-arid shrub land and acacia savannah, which is a habitat that likely supports lower insect biomass than the wet tropics of the New World (Lomolino et al. 2006). Comparing the arid and wet tropics, it seems likely that productivity is the main limiting environmental factor for sociality in *Stegodyphus* spiders in less productive habitats. However, for spiders living in wet parts of the tropics, which are also highly productive, rain damage might impose a larger force on grouping tendencies, as we suggested here for *Anelosimus*. Moreover, it might be that insects grow larger in more productive habitats, so that biomass per se is not a limiting factor for the New World social *Anelosimus* spiders.

On a local scale within few micro-habitats and for a smaller subset of species, it has been shown that social *Anelosimus* species are distributed where insect prey on average is of a larger size—but not necessarily more abundant (Guevara and Avilés 2007; Powers and Aviles 2007). This result points to cooperative foraging as a benefit of group living if cooperation allows an increase in dietary niche width (Guevara et al. 2011; Majer and Holm, unpublished data). This is consistent with foraging benefits underlying group hunting in social mammals (Davies et al. 2012). Furthermore, prey size is hypothesised to correlate with the occurrence of permanent sociality in *Anelosimus* only at relatively low altitudes and latitudes, introducing yet another set of gradients that may influence the tropical distribution of social spiders (Nentwig 1985). In addition, there are data suggesting that permanently social *Anelosimus* species are restricted to tropical lowland areas, while subsocial and solitary species reach higher latitudes and altitudes (Avilés et al. 2007; Purcell and Avilés 2008). These studies introduce the potential importance of interactions between altitude/latitude and insect prey abundance and/or body size, which requires substantial sampling at a local scale to demonstrate.

Secondly, in relation to prey availability, we hypothesised that relatively low precipitation seasonality correlates with continuous insect food supply and thus facilitates group living. This hypothesis has grounds in seminal works of Janzen and Schoener (1968) and Wolda (1978), showing that insect population fluctuations co-vary with variation in precipitation in the Neotropics. Our assumption was that phenology of insect populations fluctuates more in more seasonal habitats also across two American continents, spanning the entire distribution ranges of American *Anelosimus*. Social spider colonies are stationary and cannot relocate their nests and capture webs; consequently, they depend on a constant level of food supply (low precipitation seasonality) at their specific location in the habitat to meet colony food demands. However, we found no support for this

scenario; in contrast, we saw very weak evidence for a positive correlation between precipitation seasonality and level of sociality. This result was inconsistent between the uni- and multivariate models including precipitation seasonality (Appendix 4) as its coefficient estimate in the univariate model was negative in agreement with our hypothesis on sociality in less seasonal habitats. The positive multi-model coefficient estimate for precipitation seasonality could possibly be caused by colinearity with other variables; however, we were unable to detect this when examining correlation coefficients and variance inflation factors (Appendixes 5 and 6). Collectively, our analyses suggest that overall prey abundance plays a more prominent role in restricting the distribution of social *Anelosimus* species on a large scale than a constant supply of food. In addition, the latter hypothesis could be better supported with new empirical data on insect phenologies across larger areas to confirm our hypothesised link of insect fluctuations with precipitation seasonality.

In this study, we used a comprehensive dataset of American *Anelosimus* species' occurrences for spatial analyses. However, unlike the widespread subsocial and well-studied social species, solitary *Anelosimus* spiders were represented by very few records. Although small, the sample of solitary species in our dataset strengthened the estimated positive effect of productivity on the occurrence of social *Anelosimus*. This suggests that solitary *Anelosimus* species occur in less productive habitats than other *Anelosimus* species. This is consistent with their distribution on other continents as well, where solitary species occur in beachfront habitats that may also be less productive (Agnarsson 2012a, 2012b). Field observations in South America, Australia, and Oceania reveal that solitary *Anelosimus* occur in open and unsheltered habitats with little vegetation compared to tropical forest (Agnarsson et al. 2006b; Agnarsson 2012b). The distribution maps (Fig. 1) indicate the absence of solitary species from the inner continental parts of the Americas. Nonetheless, perhaps due to the less conspicuous appearance of solitary spiders, this could reflect incomplete sampling of species and ranges rather than a genuine characteristic of solitary *Anelosimus*.

Conclusions

We tested three environmental factors as possible drivers of macroecological patterns of sociality in 21 *Anelosimus* spiders across two continents. Our results corroborate two hypotheses explaining the geographical distribution of social species across the Americas: social species occur in areas of higher precipitation, which is consistent with better survival of groups that are better protected in large nests. In addition, social species occur in more productive areas that support more abundant food and/or larger insect prey populations

and hence sufficient prey biomass to support permanently social and immobile groups. Precipitation seasonality was not supported as a strong predictor of group living.

The predictive power of productivity was less strong for New World *Anelosimus* that occur in the wet tropics than for the Old World *Stegodyphus* spiders, for which higher productivity was the strongest predictor of social species' distribution. Within the tropical Americas, productivity may overall be sufficiently high to meet the group requirements of social species. High insect biomass correlating with wet, productive environments in the Neotropics relative to Africa–India also explains the low/lacking importance of seasonality in the former area, which is where social *Anelosimus* occur. We conclude that annual precipitation and, to some extent, gradients of productivity predict the occurrence of group-living *Anelosimus* spiders compared with non-social species, while more data and/or other explanatory variables are needed to describe solitary species' distribution ranges.

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