Symposium

Macroecology of Sexual Selection: A Predictive Conceptual Framework for Large-Scale Variation in Reproductive Traits*

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abstract: Abiotic factors exert direct and indirect influences on behavioral, morphological, and life-history traits. Because some of these traits are related to reproduction, there is a causal link between climatic conditions and the expression of reproductive traits. This link allows us to generate predictions on how reproductive traits vary in large geographic scales. Here we formalize this macroecological framework, present some general predictions, and explore empirical examples using harvestmen as study organisms. Our results show that the length of breeding season in harvestmen is primarily influenced by the number of warm months and that precipitation plays a secondary role in modulating the period devoted to reproduction. Moreover, we show that the probability of resource defense polygyny increases with longer breeding seasons and that the presence of this type of mating system positively affects the magnitude of sexual dimorphism in harvestmen. Finally, the presence of postovipositional parental care is also influenced by the length of breeding season but not by actual evapotranspiration, which is our proxy for the intensity of biotic interactions. We argue that the macroecological framework proposed here may be a fruitful field of investigation, with important implications for our understanding of sexual selection and the evolution of reproductive traits in both animals and plants.

Keywords: biotic interactions, life-history trade-offs, mating system, parental care, precipitation, sexual dimorphism, temperature.

Introduction

The exuberant variety of animal life forms in the tropics, with their many shapes, sounds, smells, and colors, have lured naturalists for centuries. Darwin himself was amazed by such diversity and was the first to suggest that many of these traits were not the result of natural selection but rather of an additional and sometimes opposite selective force he called sexual selection (Darwin 1871). Does this imply that sexual selection is stronger in the tropics when compared with temperate or cold regions? Although sexual selection is most likely affected by environmental conditions that follow geographical patterns, behavioral ecologists and evolutionary biologists are still unable to answer these kinds of questions. Moreover, considering that a great deal of the empirical studies on sexual selection have been conducted under controlled laboratory conditions and that fieldwork on the subject is still concentrated in temperate regions, it is not surprising that the gap of information on species from other parts of the globe hampers any generalization about large-scale patterns (Macías-Ordóñez et al. 2013).

There seems to be a widespread view that also constrains the potential to address large-scale evolutionary questions: the notion that the tropics are a homogeneous region where temperatures are warm, precipitation is high, and the benign environmental conditions permit the growth of tropical rain forests, with rich flora and fauna. This oversimplification has already been pointed out long ago by Darlington (1958), who acknowledged that "many definitions are possible and no simple one is entirely satisfactory, for the tropics vary in climate (wet to dry), vegetation (rain forest to desert), and animal life" (p. 492). In fact, the tropics have been defined in many very different ways, and thus their limits vary depending on the discipline and criteria considered (Macías-Ordóñez et al. 2013). Interestingly, there is another oversimplification when "temperate" is defined as anything "nontropical," thus ignoring a wide variety of environmental conditions that include not only temperate but truly cold regions. As shown in figure 1, both tropical and temperate regions include a great mosaic of climate types,

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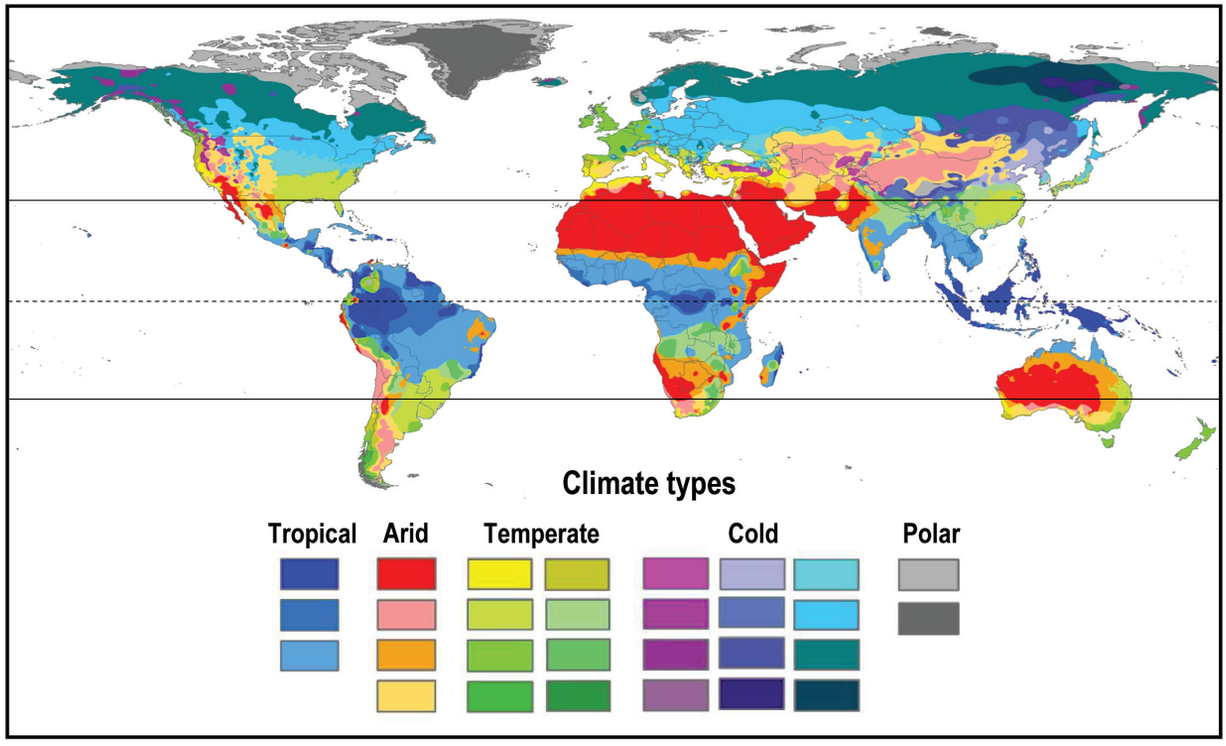

Figure 1: Köppen-Geiger climate classification map (modified from Peel et al. 2007). The aim of this figure is to show that climate types (identified with different colors) hardly follow a latitudinal pattern in large continental areas, such as southwestern North America, western South America, and central Asia, where complex topography influences temperature and precipitation patterns, resulting in an extremely patchy distribution of environmental conditions. In these large areas, latitude alone would represent only a small fraction of the variance of climatic conditions, resulting in a poor proxy for them. The dashed line crossing the equator, for instance, intercepts eight climate types, which are tightly associated with biomes as different as deserts (red areas) and tropical rain forests (dark blue areas). The solid lines indicate the limits of the tropical region, where a mosaic of climate types, ranging from hot-humid to mild-dry, can be found. An even greater diversity of climate types is found outside the tropical region, the region we call temperate.

which are clearly not distributed along a simple latitudinal gradient.

If we are interested in the study of selective forces shaping reproductive traits on a large geographic scale, it is necessary to be specific about the environmental conditions shaping those forces. Climate probably offers the most independent array of environmental variables influencing the forces of natural and sexual selection. Therefore, by using climatic variables, we may gain more insights into the selective forces shaping reproductive traits, thus avoiding the so-called temperate assumptions. This notion has recently been explored in the first chapter of the book *Sexual Selection: Perspectives and Models from the Neotropics*, where Macías-Ordóñez et al. (2013) proposed a macroecological framework for studying the large-scale influence of climate on reproductive traits. Rather than simply searching for global patterns, the aim of the chapter was to propose a hypothesis-driven approach of testing observations against predictions on how reproductive traits should vary across large geographical scales. These predictions were mostly based on information provided by small-scale studies on physiology, life history, and mating systems.

Here we revise and update this macroecological framework in order to make it available for a broader audience. Additionally, we provide empirical examples of the hypothetico-deductive approach, in which we investigate the possible influence of environmental factors on the reproductive biology of a diverse arthropod group, the order Opiliones. For this major arachnid group, we have a data set on the length of breeding season, type of mating system, magnitude of sexual dimorphism, and presence or absence of postovipositional parental care for a large and representative sample of species widely distributed in many climate types. With the working examples, we intend to show that the macroecological framework provides a fruitful field of investigation, with important implications for our understanding of sexual selection and the evolution of reproductive traits.

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Macroecology of Sexual Selection

The great majority of macroecological studies investigate large-scale spatial variation in species richness, abundance, distribution, and body size (Ricklefs and Schluter 1993; Gaston and Blackburn 2000). The main explanation for some of the large-scale patterns found in these macroecological studies is directly connected to variation in physiological responses (Chown and Nicolson 2004). For instance, interspecific differences in the limits of tolerance to abiotic factors have been considered one of the most important factors to explain the taxonomically widespread pattern of latitudinal decrease in species richness (Willig et al. 2003). According to Stevens (1989), species from high latitudes have wider tolerance to climatic variability than species from low latitudes. Therefore, species from high latitudes have few constraints to expand their lower limits of distribution, whereas species from low latitudes are constrained by their upper limits of distribution. The predicted consequence of this hypothesis is an inflation of species richness at low latitudes through greater emigration rates of species from high latitudes (Pintor et al. 2015). Explanations for macroevolutionary patterns in body shape and size—namely, Allen's rule and Bergmann's rule—also rely on physiology. Allen's rule states that endotherms from colder climates have relatively shorter limbs than their relatives from warmer climates, whereas Bergmann's rule states that animal species from colder climates are larger than their relatives from warmer climates. A decrease in the surface-volume ratio increases heat conservation in species from colder climates, explaining the macroecological variation in both relative limb length and body size (Gaston and Blackburn 2000).

Perhaps one of the most intensively studied morphological traits in any animal group is sexual size dimorphism, which has been approached under macroevolutionary and macroecological perspectives since the nineteenth century (Fairbairn 2007). Rensch's rule, for instance, states that the body size of the larger sex varies, or evolutionarily diverges, more than the body size of the smaller sex among species within a lineage. This allometric pattern has already been demonstrated for several animal groups, including vertebrates and invertebrates (examples in Fairbairn et al. 2007). Recent studies on phenotypic plasticity have also shown that populations of several arthropod species experiencing different temperatures in nature exhibit marked differences in sexual size dimorphism, even when there is no genetic differentiation in size among populations (Stillwell et al. 2010). Regardless of the cause, the consequences of geographic variation in sexual size dimorphism in terms of sexual selection remain poorly explored.

In contrast to the large-scale studies investigating variation in ecological or morphological attributes exemplified above, studies investigating how reproductive or sex-specific traits vary geographically in response to environmental factors are comparatively scarce (Macías-Ordóñez et al. 2013). Most of the multispecies macroecological studies focusing on reproductive traits have been conducted with vertebrates, including fish (Conover 1992), amphibians (Gomez-Mestre et al. 2012), mammals (Ebensperger et al. 2012), and especially birds (Cardillo 2002; Pienaar et al. 2013; Lawson and Weir 2014; Dale et al. 2015). Latitudinal variation in clutch size and incidence of cooperative breeding in birds, for instance, has long been debated. Several environmental factors have been evoked to explain the evolutionary causes of intra- and interspecific clutch size variation, including predation pressure, seasonal variation in resource availability, abiotic factors that limit adult populations during the nonreproductive period, and heat exchange between eggs and the environment (Martin et al. 2000; Ricklefs 2000; Cooper et al. 2005 and Jetz et al. 2008). Cooperative breeding, in turn, is usually explained by low annual adult mortality, which is associated with increasing sedentariness and decreased environmental fluctuation (Arnold and Owens 1998; Jetz and Rubenstein 2011).

Although empirical studies of clutch size and cooperative breeding in birds provide clear evidence of broadscale variation in reproductive traits, most seek to understand the underlying processes using the simplistic dichotomy between temperate and tropical regions or, at best, using latitude as an explanatory variable. There are some exceptions, such as the article by Ricklefs (1980), who provides a test for Ashmole's (1963) hypothesis, according to which clutch size in birds should vary in direct proportion to the degree of seasonal fluctuation in the level of resources utilized by a population. The author showed that clutch size is inversely related to the ratio between winter and summer actual evapotranspiration (a proxy of primary production). More recently, Jetz et al. (2008) tested how biotic and abiotic factors influence clutch size in birds. They found that clutch size is consistently larger in cavity nesters and in species occurring in seasonal environments, which provides additional support to Ashmole's (1963) hypothesis. Finally, Jetz and Rubenstein (2011) showed that between-year environmental variability in precipitation is an important predictor of the incidence and distribution of cooperative breeding in birds. Taken together, the findings reported in these three studies reinforce the notion that if we want to understand the macroecology of reproductive traits, we need to be explicit about the selective pressures that may shape these traits. Moreover, they also illustrate the hypothesis-driven macroecological approach that we are going to develop hereinafter.

Abiotic factors may exert both direct and indirect influences on behavioral, morphological, physiological, and life-history traits (Bradshaw 2003; Chown and Nicolson 2004). At least some of these traits are directly or indirectly related to reproduction and are under sexual selection. We argue that

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life-history theory offers a good starting point for a predictive framework on how large-scale variations in environmental conditions may influence reproductive traits (Ricklefs and Wikelski 2002). According to this theory, limited resources must be partitioned into three main fitness components: (1) somatic effort, comprising actions that increase individual development, maintenance, and survival; (2) mating effort, comprising actions to acquire sexual partners; and (3) parental effort, comprising actions that increase offspring fitness (Magrath and Komdeur 2003). An increase in the resources allocated to one of these fitness components implies a decrease in the resources allocated to one or both of the other components (Roff 2002). Therefore, individuals should be selected to maximize their lifetime reproductive success by optimizing resource allocation to these three components in each breeding attempt. Any environmental factor that changes the fitness profit for one component will have a direct effect on the other components. For example, if climatic seasonality constrains the breeding season to only a few months, the net benefit of mating effort compared with parental effort is expected to be higher because caring activities are usually time-consuming and males may increase their reproductive success by allocating more time and/or energy into searching for mating partners.

Another possible connection between environmental conditions, life history, and reproduction is the effect of parasitism on sexually selected traits. There is some empirical evidence that parasitism is more prevalent in hot-humid climates (Schemske et al. 2009). Considering that resistance and immune response against parasites are costly (whether alone or in combination) and may impose resource allocation trade-offs, other fitness components, such as mating effort, may be compromised when parasitism is intense (Lawniczak et al. 2007). In insects, for instance, the main immune response involves encapsulation of the parasite via the phenoloxidase cascade and subsequent melanization of the encapsulated parasite (Schmid-Hempel 2005). The same biochemical precursors involved in immune response are also responsible for melanin-based, sexually selected ornaments, such as wing pigmentation in odonates (Siva-Jothy 2000). Therefore, simultaneous investment in immune defense and sexual displays may impose allocation trade-offs (Zuk and Stoehr 2002). Similar allocation trade-offs also occur with the carotenoid-based sexual ornaments of many birds (Baeta et al. 2008) and fish (Clotfelter et al. 2007). Contrary to the melanin-based ornaments of insects, carotenoids are obtained exclusively from the diet but are also used to enhance immune response (Olson and Owens 1998; Blount et al. 2003; McGraw and Ardia 2003). All else being equal, the macroecological prediction is that males from sites where parasitism is more intense (probably hot-humid climates) should be more ornamented because melanin- and carotenoid-based sexual ornaments may signal immunocompetence.

Finally, mating system theory also provides a fruitful theoretical background for understanding large-scale variations in reproductive traits. The distribution and limitation of key resources for reproduction in time and space predict the optimal set of mating strategies in a population (Emlen and Oring 1977; Shuster and Wade 2003). As mentioned above, strong climatic seasonality may constrain the length of breeding season to only a short period, during which high synchrony in mating activity should be expected. Among univoltine species, for instance, individuals that take longer to be sexually mature can lose mating opportunities (mostly males) and have less time to eat and produce gametes (mostly females). In this situation, males and females should be selected to be reproductively active at the same time, and even males with high competitive ability may have limited opportunities to monopolize a great number of females, so that variance in male reproductive success should be low (Ims 1988; Grant et al. 1995). In contrast, a longer breeding season may allow females to be reproductively active in an asynchronous manner, so that the most competitive males may be able to sequentially monopolize a much larger number of females, which leads to higher variance in male reproductive success. Additional predictions will be explored in more detail below, and our goal here is just to highlight that climatic conditions may affect the relative amount and diversity of available resources, as well as their temporal and spatial distributions. Therefore, we expect different selective pressures on reproductive strategies under different climatic regimes and, thus, variation in mating systems and a whole array of aspects associated with reproductive ecology. These include, among others, the length of breeding season, the type of mating system (i.e., the strategy of mate acquisition and the amount and distribution of time allocated to parental care), and the degree of sexual dimorphism.

Macroecological Predictions

Based on the macroecological framework presented above, we now develop general predictions within a bidimensional environmental matrix composed of two interacting variables: temperature and precipitation. This matrix contains the following four extreme conditions and all possible intermediate states: hot-humid, hot-dry, cold-humid, and cold-dry. Some broad environmental gradients may be suggested in this bidimensional space covering most climatic conditions. Energetic demands, for instance, should be higher in cold climates compared with regions where temperatures are closer to those required for metabolic processes (Willmer et al. 2000). This may have consequences for self-maintenance and reproductive effort, as well as for offspring demands and mortality. Water loss in drier areas also results in physiological constraints that may shape self-maintenance and reproduction, especially in water-sensitive groups, such as amphib-

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ians and many arthropods. An overall abundance of resources may be expected in regions with hot-humid climates due to higher energy and water and nutrient availability (Moya-Laraño 2010), which may result in higher food input and an overall attenuation of life-history trade-offs (Harshman and Zera 2007). Finally, biotic interactions seem to be more important in hot-humid climates, where vector-borne parasites, pathogenic diseases, and predation are probably more frequent or intense (Schemske et al. 2009).

Regardless of mean annual temperature and precipitation at a given area, both climatic variables have region-specific patterns of seasonality that dictate the combination of environmental conditions that result in actual selective pressures. Mean annual temperature and temperature seasonality are highly correlated, because both covary with distance to the equator. Annual precipitation and precipitation seasonality, however, may be more independent from each other as they result from a wide and somewhat different array of geographical factors. As a result, when building detailed macroecological predictions on reproductive traits, it may be appropriate to consider environmental variables along three somewhat independent main axes: one related to temperature that implies an unavoidable correlation between mean annual temperature and temperature seasonality, one representing the amount of precipitation, and another representing the temporal distribution of precipitation. The selection of these axes may be dictated by group-specific physiological constrains. Temporal distribution of rainfall, for instance, may be assumed to play a relatively unimportant role in some groups not highly dependent on water but a prominent one in other groups with life histories tightly tied to pulses of water availability.

Macías-Ordóñez et al. (2013) derived specific macroecological predictions for three groups of land animals, namely, arthropods, ectothermic vertebrates, and endothermic vertebrates. For the sake of conciseness, here we focus on land arthropods, which include representatives of four major groups: insects, arachnids, myriapods (centipedes and millipedes), and crustaceans of the order Isopoda (woodlice). These groups comprise the great majority of species in terrestrial environments, and there is no doubt that the diversity of their morphologies and behaviors can prevent generalizations. Nonetheless, arthropods share general features that allow us to predict how they respond physiologically to temperature and precipitation. For example, water loss rates in arthropods vary with relative humidity, which is highly correlated with total rainfall. Moreover, there is a negative relationship between standard metabolic rate and environmental temperature. These patterns of variation would not be detectable if arthropods showed a wide array of physiological responses to the environment. Thus, despite all variation associated with feeding habit, age, and body size in arthropods, there is growing evidence that a considerable proportion of the variation in physiological traits is partitioned at high taxonomic levels, such as family or order (Chown and Nicolson 2004). Some of these phylogenetically conserved physiological traits are directly or indirectly related to reproduction, which allows us to derive large-scale predictions about the effects of climate on reproductive traits, including both morphology and behavior. These predictions, however, should be viewed mostly as examples of the hypothetico-deductive approach we are proposing. Whenever possible, specific information on the ecology and natural history of the study group should be used to strengthen the predictive power of the macroecological framework (see examples in the section "Macroecology of Harvestman Mating Systems").

Just as they affect many other animal groups, abiotic factors, such as low temperatures, limit the occurrence of arthropods in cold climates. Although some species have specialized physiological mechanisms to resist freezing temperatures during cold periods, most species go through their entire life cycles in the warm months, when they grow fast, reproduce, and eventually die (Chown and Nicolson 2004). A short period of favorable climatic conditions probably constrains developmental time, leading to fast sexual maturity and small body sizes in annual species. Therefore, time-consuming activities, such as postovipositional parental care, are expected to be rare. Semelparity should be the rule, and females should lay a large number of eggs, hiding them in protected places, where they will probably overwinter (Tallamy and Schaeffer 1997; Tallamy and Brown 1999; Machado and Raimundo 2001). A final consequence of a short breeding season, when a large number of individuals are reproductively active at the same time, is that the most frequent mating system should be a scramble competition polygyny. As predicted by theory, a large number of males within the searching area makes territoriality unprofitable (Emlen and Oring 1977; Thornhill and Alcock 1983). Moreover, an experimental study with a beetle species has shown that smaller males—that is, those that probably developed at faster rates—are better scramble competitors at cooler temperatures (Moya-Laraño et al. 2007). This result, obtained under laboratory conditions, suggests that climate may also have an important role in influencing male development, size, and mating success in the field.

At the other extreme, species living in regions with hot-humid climates, with abundant resources throughout the year, are probably subject to intense predation and fungi infection on eggs, which may increase the benefits of postovipositional parental care in terms of offspring protection against natural enemies (Wilson 1975). Moreover, high temperatures should accelerate embryonic development, so that the foraging costs associated with a long period of parental care are expected to be low. For predators, which are generally food-deprived while caring for offspring (Thomas and Manica 2003), parental care is expected to be followed by

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a fast period of production and maturation of new eggs as a direct consequence of abundant food sources. Even for species that do not exhibit any form of postovipositional parental care, favorable and stable climatic conditions should favor iteroparity so that individuals may have several reproductive events throughout the year. Because the breeding season is long, there would be no selective pressure favoring reproductive synchrony, and at any given moment, populations should be composed of both receptive and nonreceptive individuals. Moreover, considering that male gametes are usually replenished faster than female gametes, a high degree of female reproductive asynchrony would result in a more male-biased operational sex ratio and potentially stronger sexual selection in species with no paternal care (Ims 1988; Shuster and Wade 2003). The most common mating system under this scenario should be some kind of resource or female defense polygyny, and male-male fights should be more frequent and/or intense (Emlen and Oring 1977; Thornhill and Alcock 1983). In fact, one of the few empirical studies using the macroecological framework presented here has shown that mean duration of male-male fights is longer in butterfly species living in areas with more stable climatic conditions when compared with species living in areas with marked temperature and precipitation seasonality, where the breeding season is usually shorter (Peixoto et al. 2014). The authors interpret this pattern as the result of higher payoffs accrued with territorial defense in areas where the breeding season is long and female receptivity is asynchronous.

Macroecology of Harvestman Mating Systems

Behavioral data accumulates at a much lower rate than data on species richness or body size, which may explain why a macroecology of reproductive traits has lagged behind in many animal groups, particularly invertebrates. Here we adopt the macroecological framework presented above and use recent techniques of phylogenetic control to understand the influence of climate on two components of the mating system, the strategy of mate acquisition and the presence of parental care, and on two traits associated with the intensity of sexual selection, the length of breeding season and sexual dimorphism. Our model organisms are representatives of the order Opiliones, commonly known as harvestmen or daddy longlegs. The order is composed of nearly 6,500 species distributed in all continents (except for Antarctica) and divided in four living suborders, namely, Cyphophthalmi, Eupnoi, Dyspnoi, and Laniatores (Machado et al. 2007; Kury 2012). Like many arthropod groups, harvestman species are absent at the lower ends of humidity and temperature ranges but are both diverse and abundant in environments with moderate-to-high temperature and humidity (Curtis and Machado 2007). The large surface/volume ratio (typical of long-legged arthropods), lack of spiracular control, and low osmotic hemolymph concentration of these species may explain why most occur in damp and shaded areas (Santos 2007).

The great majority of harvestman species reproduce sexually and are highly polygynandrous, so that both males and females copulate with multiple mates throughout the breeding season (Machado and Macías-Ordóñez 2007). The most common mating system in harvestmen seems to be scramble competition polygyny (Buzatto et al. 2013). In many species studied so far, females lay eggs on sites that cannot be profitably monopolized by males, such as the bark of trees and leaf litter (Machado et al. 2015). Another widespread mating system in harvestmen is resource defense polygyny, in which males fight each other for the possession of reproductive territories that are visited by females looking for particular oviposition sites (Buzatto and Machado 2014). The reproductive territories include natural cavities on trunks and riverside banks, rocks, specific host plants, and mud nests built by males. In some species, females remain inside the male's territory after oviposition, forming harems, whereas in other species, females abandon the male's territory after oviposition, leaving their eggs either hidden inside small cracks in the substrate or under the male's guard (Machado et al. 2015). Postovipositional parental care has evolved many times independently in the suborder Laniatores, with both exclusive maternal and paternal care being reported for many species. The main benefit provided by the parents is protection against egg predators, but in at least one species, caring males can actively clean the eggs and prevent fungal infection (Machado and Macías-Ordóñez 2007).

Although our understanding of harvestman reproduction is still incipient in many aspects (Machado et al. 2015), there is enough information on reproductive phenology, mating system, sexual dimorphism, and postovipositional parental care for a great number of species occurring in different climate types worldwide to allow comparative analyses. The group, therefore, offers a good opportunity to test macroecological predictions. In fact, preliminary analyses have already been conducted by Buzatto et al. (2013), who investigated the role of temperature and precipitation on the length of breeding season and on the presence of postovipositional parental care in harvestmen. Here we revisit these same questions with a larger number of species and reanalyze the data using continuous climatic variables rather than climate types. This reanalysis also includes more information on harvestmen physiology (see below), so that the connection between process and pattern, which is the philosophical basis of our macroecological framework, has been strengthened. Moreover, we included new analyses on the role of breeding season length in the type of mating system and the magnitude of sexual dimorphism. All the analyses presented here greatly benefited from recent phylogenies for some taxa whose internal relationships were previously obscure.

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Length of Breeding Season

Reproduction is universally triggered by environmental conditions, and arthropods are no exception. Despite the incredible diversity of arthropod species, reproductive activities, such as courtship, mating, oviposition, and postovipositional parental care are frequently concentrated in the period of the year with adequate environmental conditions for adult activity. Therefore, climate should have a marked effect on the length of breeding season in the group (Wolda 1988; Corbet et al. 2006). In order to create macroecological predictions for the length of breeding season in harvestmen, we need first to know how temperature and humidity influence adult activity and survival. There are only a few physiological studies on this subject, but the results they report are highly consistent, regardless of species or region of the study (table A1; tables A1–A5 available in the online appendix).

Although harvestman eggs and sometimes early hatched nymphs are remarkably resistant to temperatures as low as −30°C, lethal temperatures for adults range from −5°C to 3°C (Cokendopher and Jones 1991; Novak et al. 2004; Punzo et al. 2007; Leirikh et al. 2009). In a few species, adults survive harsh winter conditions with temperatures below freezing point, but in all these cases, individuals hide or hibernate in protected places, such as inside caves, where temperatures are consistently higher than the external environment (Belozerov 2012). Moreover, studies on temperature preference for several harvestman species worldwide, including representatives from both hot and cold climates, show that adults have a preference for warm temperatures, with a mean of 18°C (range = 3.4°–29°C; $n = 22$ species; table A1). Taken together, these results indicate that low temperatures severely limit adult activity and survival and, consequently, will have a major role in determining the period of reproductive activity.

The length of breeding season in harvestmen may also be modulated by precipitation, which greatly determines air humidity. As mentioned above, harvestmen are particularly sensitive to dehydration; eggs, nymphs, and adults die within a few hours or days if maintained under constant dry conditions (Todd 1949; Edgar 1971; Hebling-Beraldo and Mendes 1982). However, it is important to note that air humidity interacts with temperature to determine dehydration stress and, thus, adult survival. At 10°C, for instance, the harvestman *Vonones ornatus* (Laniatores) from southern Florida lives on average 2.8 days under 12% of relative humidity (a measure of water saturation of the air, which is temperature dependent), whereas average survival at the same temperature but under 70% of relative humidity reaches 11.7 days (Punzo et al. 2007). Therefore, high precipitation may improve adult activity and survival regardless of temperature by increasing air humidity and, thus, decreasing water loss. Based on our knowledge of harvestmen physiology, we predict that the number of months with mean temperature above the lower lethal limit defines the phenological window of adult activity and, consequently, the potential period for reproduction in harvestmen. Within the phenological window of adult activity, we predict that the actual length of breeding season is modulated by overall precipitation, so that populations or species living in wet places will have longer breeding seasons when compared with their relatives living in dry places.

We used the information on harvestmen physiology presented above to make informed decisions on how to use climatic data to generate appropriate explanatory variables for our comparative analyses. Based on the reasoning that the main constraint to adult activity in harvestmen is temperature, we used the number of months with average temperature higher than a minimum threshold as our first climatic variable, which will hereafter be referred to as favorable months. We repeated our analyses with the minimum thresholds of 5°C and 10°C to assess the sensitivity of our results to the threshold chosen. Once we defined the favorable months, we calculated the average monthly precipitation during this period, which was our second climatic variable. Because sensitivity to dehydration can modulate harvestmen resistance to stressful temperatures, we predict that the length of breeding season in the group will be determined by an interaction between the number of favorable months and the average precipitation during these months.

We gathered data on the length of breeding seasons by searching the literature on harvestmen biology and contacting several experts on the group to obtain additional information. From each article, we extracted the geographic coordinates of the population studied; when coordinates were not available in the article, we used Google Maps (https://maps.google.com) to obtain this information. Then, we used WorldClim (http://www.worldclim.org) to obtain two climatic variables for each locality: (1) the number of favorable months, that is, those with an average temperature equal to or higher than the minimum threshold for harvestmen adult activity (5°C or 10°C, henceforth, T5 and T10, respectively); and (2) the average monthly precipitation during the favorable months, considering the total precipitation accumulated in this period (PP5 for T5 and PP10 for T10). Our data set on the length of breeding seasons includes 94 species belonging to 17 families and all four living suborders of Opiliones. For 11 species, we found information for multiple populations (two or three), leading to a total of 107 populations spread across all continents (except Antarctica) and a large variety of climate types (table A2). We then inferred the phylogenetic relationships among the species included in our data set based on several molecular and morphological phylogenies (fig. A1*a*; figs. A1–A4 available in the online appendix; Nexus file in part 1 of the additional supplements, available online). Given that morphological phylogenies do not provide information on branch length, we set all branch

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lengths to 1. Whenever different phylogenies disagreed in relation to the position of a given taxon, we used polytomies to indicate lack of information. Whenever we had information on different populations of the same species, we also used polytomies and set branch lengths to 0.1, given that such populations must be more closely related to each other than sister species. We checked the effect of this assumption on our results by reanalyzing the data after setting branch lengths of conspecific populations to 1, 0.01, or 0.001. Because the patterns obtained with all branch lengths were qualitatively the same (data not shown), we present here only the results regarding between-population branch length = 0.1.

Prior to the comparative analyses, we standardized the variables of temperature (T5 and T10) and precipitation (PP5 and PP10) to the same scale by centering their means to zero and making their variances uniform by dividing variables by two times their standard deviations. This standardization procedure improves model convergence and aids the comparison of coefficients (Gelman 2008). Next, we used model selection to analyze the influence of the standardized variables and their interaction on the log-transformed proportion of the year each species was reproductively active (i.e., the length of their breeding seasons). First, we built a set of candidate models that included a null model, three models with every possible combination of the fixed effects (T5/PP5 or T10/PP10), and the fully parameterized model that included both fixed effects and their interaction. Then, we ranked the five models on the basis of the bias-corrected version of the Akaike information criterion (AICc; Burnham and Anderson 2002).

We fit all models with phylogenetic generalized least squares (Nunn 2011) as implemented in the function pgls (Freckleton et al. 2002) from the package caper (Orme et al. 2013) in R, version 3.1.3 (R Development Core Team 2015). This approach is based on calculating the level of phylogenetic dependence between data points through maximum likelihood and then taking this parameter (λ) into account when fitting a linear model to the data (Pagel 1999; Ives and Garland 2010). Finally, we checked the best model for normality of residuals by simulating 1,000 normal distributions with the same mean, standard deviation, and sample size of the residuals from our model and testing these distributions against the actual residuals with Kolmogorov-Smirnov tests. We considered the residuals normally distributed if these tests failed to detect significant differences in at least 90% of the simulated distributions. We also checked the minimal most likely model for multicollinearity using the function corvif (Zuur et al. 2009) and for heteroscedasticity using the function fligner.test, all in R, version 3.1.3 (R Development Core Team 2015). The scripts of the analyses can be found in part 2 of the additional supplements.

The most likely model was the fully parameterized one for both the analysis using T5 and PP5 and the analysis using T10 and PP10 (ΔAICc = 10.97 and ΔAICc = 2.58, respectively, with the second-most likely model). These fully parameterized models include the temperature and precipitation variables, as well as their interaction (table 1; fig. 2). Both variables positively influenced the length of breeding season in harvestmen, but as expected from our predictions, the effect of the number of months with favorable temperature was stronger than the effect of the average precipitation in these months (fig. 2). However, an adequate interpretation of these effects can be achieved only by taking into account the significant interaction between the two variables,

Table 1: Model selection for the effects of climatic conditions on the length of breeding season of 94 harvestman species

Threshold, fixed effects	Log likelihood	k	AICc	ΔAICc	AIC weights	Cumulative weights
Threshold of 5°C:						
T5 + PP5 + T5:PP5	**−81.35**	**4**	**171.08**	**…**	**.99**	**.99**
PP5	−88.97	2	182.06	10.97	.00	1.00
T5 + PP5	−88.16	3	182.56	11.48	.00	1.00
Null (intercept only)	−91.56	1	185.15	14.07	.00	1.00
T5	−91.28	2	186.68	15.60	.00	1.00
Threshold of 10°C:						
T10 + PP10 + T10:PP10	**−83.14**	**4**	**174.66**	**…**	**.75**	**.75**
T10 + PP10	−85.50	3	177.24	2.58	.21	.96
T10	−88.36	2	180.84	6.18	.03	.99
PP10	−90.09	2	184.30	9.64	.01	1.00
Null (intercept only)	−91.56	1	185.14	10.49	.00	1.00

Note: Fixed effects used were (i) the number of months with average temperature higher than a minimum threshold of 5°C (T5) or 10°C (T10), (ii) average precipitation during those months (PP5 or PP10), and (iii) their interaction (T5:PP5 or T10:PP10). Log likelihood = the natural logarithm of the maximum likelihood; k = the number of estimable parameters; ΔAICc = the difference between the corrected Akaike information criterion (AICc) of each model and the AICc of the first model; AIC weights = the Akaike weights of each model; cumulative weights = the cumulative Akaike weights of each model and the models above it. Models are ranked by increasing AICc values, and the minimal most likely model is indicated in boldface. All models were fit with phylogenetic generalized least squares.

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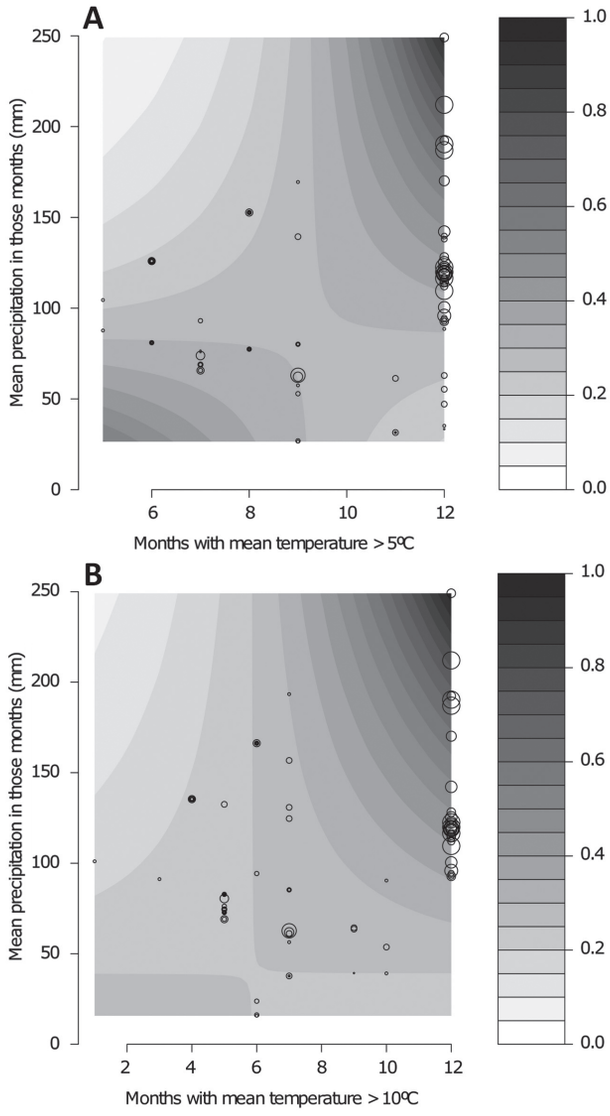

Figure 2: Length of breeding season in harvestman species is influenced by an interaction between the number of months with average temperatures equal to or higher than the minimum threshold for adult activity (*A*, 5°C; *B*, 10°C) and the average monthly precipitation during those months. The data shown are the length of the breeding season as a proportion of the year, thus varying from 0 to 1. Shades of gray represent the predicted values from the minimal most likely model (see table 1), and the size of the open circles is proportional to the actual (rather than predicted) length of breeding season in each population.

which was stronger in the analysis with T5 and PP5 than in the analysis with T10 and PP10. The effect of the number of months with favorable temperature was more important when these months had at least 70 mm of average monthly precipitation. Likewise, the effect of average precipitation was more important when there were at least 6 months of favorable temperature (fig. 2). The level of phylogenetic dependence on the length of breeding season was estimated to be 0.58 and 0.33 for the analyses using the minimum temperature thresholds of 5°C (variables T5 and PP5) and 10°C (variables T10 and PP10), respectively.

The dominant effect of the number of months with favorable temperature (T5 and T10) on the length of breeding season in harvestmen was to be expected because when average temperature is higher, thermal seasonality is weaker. When this period is long enough, however, humidity seems to play a more significant, but still secondary role. Conversely, the effect of temperature on the length of breeding season is weaker in drier environments, illustrating how low humidity may become a more relevant physiological constrain for reproduction in such areas than temperature. Overall, species in hot-humid versus cold-dry places seem to have, respectively, very long versus very short breeding seasons, more so than would be expected from the independent effects of temperature and precipitation. This interaction seems to be even stronger when we include the temperature range between 5°C and 10°C (T5 : PP5 versus T10 : PP10; table 1), in which most harvestmen (or most arthropods) may still show adequate physiological performance in terms of maintenance, but probably few will perform energetically costly functions involved in reproduction, such as mate search, territorial defense, or gamete production. The temperature values used here, however, must be considered as proxies, because standard conditions in which climatic data are recorded are likely to differ from those experienced by the study species. In the case of harvestmen, in which individuals are usually closely associated to the substrate, microclimatic conditions probably result in a few degrees more than the recorded or modeled temperature for each site due to the thermal buffer effect of the substrate (especially the leaf litter).

Mating System and Sexual Dimorphism

As stated before, species or populations in cold-dry environments with short breeding seasons will most likely experience high breeding synchrony, which should result in scramble competition polygyny because males would be unable to monopolize females or the resources they need to reproduce. Conversely, in hot environments, especially where humidity (precipitation) is high, we expect longer breeding seasons and, thus, different degrees of breeding asynchrony. This situation may lead, in combination with other demographic variables such as sex ratio or overall individual density, to a variety of mating systems, more frequently associated with female or resource defense. Given that female or resource defense necessarily involves male-male aggressive interactions (Andersson 1994), populations or species inhabiting hot-humid environments should exhibit more pronounced male-biased sexual dimorphism, not only in body

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size but also in a wide variety of male structures used as weapons in intrasexual contests (examples in Emlen 2008). On the other hand, populations or species inhabiting cold-dry environments and exhibiting a scramble competition polygyny should be less sexually dimorphic, and male weaponry should be poorly developed or even completely absent. Therefore, climate may have an important effect both on the type of mating system (via length of breeding season) and the magnitude of sexual dimorphism (via type of mating system) of many species. Here we used behavioral and morphological data on a large number of harvestman species to test these macroecological predictions.

Although field studies specifically devoted to describe harvestman mating systems are relatively scarce ($n = 5$ species), behavioral information on many species ($n = 46$) are sufficiently detailed to provide a reasonable categorization of their mate-acquiring strategy into either scramble competition or resource defense polygyny (table A3), which are the two most common mating strategies in the order (Buzatto et al. 2013; Machado et al. 2015). Following the rationale described above, we investigated the potential positive effect of the length of breeding season on the probability that a harvestman species or population will present a resource defense polygyny, as opposed to the more common scramble competition polygyny. We once again tested this prediction with phylogenetic comparative methods, this time comparing a model with the length of breeding season as the sole explanatory variable against a null model (which had only the intercept) through their AICc values. Both models had resource defense polygyny (1) or scramble competition polygyny (0) as a binomial response variable and were fit with phylogenetic logistic regression as implemented in the function phyloglm from the package phylolm (Ho and Ané 2014) in R, version 3.1.3 (R Development Core Team 2015). This function also calculates the level of phylogenetic dependence between data points (Pagel 1999; Ives and Garland 2010) through maximum likelihood and takes it into account when fitting generalized linear models to the data. Finally, we checked the best model for overdispersion by dividing the model's residual deviance by its residual degrees of freedom.

We gathered information about the mating system of 59 populations (51 species) for which we had data on the length of their breeding seasons, including representatives of the four living suborders of Opiliones distributed across the Americas, Europe, Asia, and Oceania. We inferred the phylogenetic relationship among species based on molecular and morphological phylogenies (fig. A1*b*; Nexus file in part 1 of the additional supplements), setting all branch lengths to 1 (except for conspecific populations, where branch lengths were set to 0.1). Polytomies indicated lack of information whenever phylogenies disagreed, and we checked the impact of branch lengths for conspecific populations on our results by reanalyzing the data with these branches set to lengths of 1, 0.01, or 0.001. Because the patterns obtained with all branch lengths were again qualitatively the same (data not shown), we present only the results with conspecific branch lengths = 0.1. The scripts of the analyses can be found in part 2 of the additional supplements.

The model that included the length of breeding season was more likely than the null model (ΔAICc = 11.87), indicating that, as expected, the probability of a species to have a resource defense mating system is higher in species with longer breeding seasons (fig. 3). The level of phylogenetic dependence on mating system type was estimated to be 0.07, suggesting that mating systems in harvestmen are extremely evolutionarily labile. In fact, two populations of *Leiobunum vittatum* (Eupnoi) inhabiting regions with different climates and availability of breeding sites in North America show marked differences in their mating systems. In the population from eastern Pennsylvania, suitable substrates for oviposition are limited to cracks in rocks, which are patrolled and defended by males, as in a typical resource defense mating system. In the population from central Michigan, climate conditions are harsher and the breeding season is nearly 1 month shorter than in Pennsylvania. Moreover, females lay eggs inside fissures on fallen trunks, which are widespread and abundant in the study site. As should

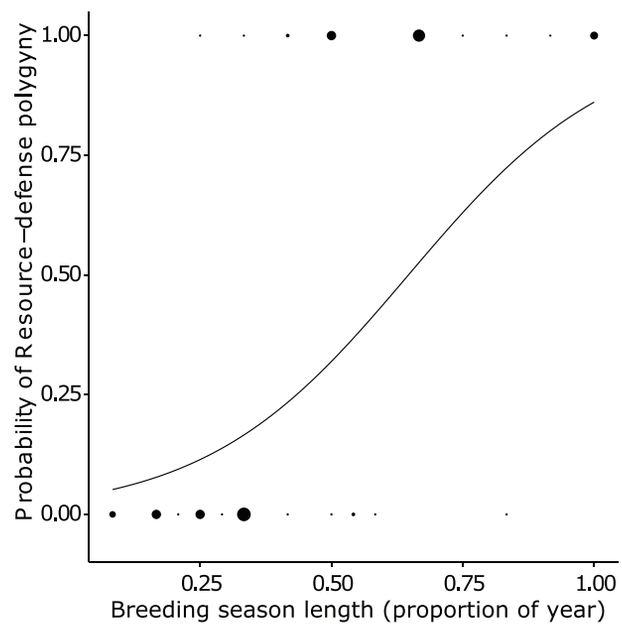

Figure 3: Probability that the mating system of a harvestman population is resource defense polygyny (1) or scramble competition polygyny (0) depends on the proportion of the year adults are reproductively active (length of breeding season). The curve represents the predicted values from our model, and the size of the closed circles is proportional to the number of species in each combination of mating system type and length of breeding season.

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be expected, the mating system in this population is a scramble competition polygyny, and agonistic interactions between males are rare (Machado and Macías-Ordóñez 2007; Buzatto et al. 2013).

After unveiling the effect of the length of breeding season on the type of mating system, we investigated the subsequent effect of the type of mating systems on the magnitude of sexual dimorphism in harvestmen. To this end, we used taxonomic descriptions and other sources of information in the literature to acquire data on sexual dimorphism in 10 morphological structures that are known to be used in male-male contests (Buzatto et al. 2014; Machado and Buzatto 2014): spines on the coxa, trochanter, femur, and tibia of the fourth pair of legs (0 = absent or same size in males and females, 1 = larger or present only in males); femur length of the fourth pair of legs, total length of the second pair of legs, and body length (0 = male ≤ female, 1 = male > female); cheliceral and pedipalpal robustness (0 = similar in males and females, 1 = larger in males); and pedipalpal horns (0 = absent in males and females, 1 = present only in males). To build an index of sexual dimorphism, we summed the scores of all body structures for each species. This index, therefore, can range from 0 (when males are totally unarmed and morphologically similar to females) to 10 (when males are heavily armed and morphologically very different from females). In total, we gathered information on sexual dimorphism for all species ($n = 51$) and populations ($n = 59$) for which we have data on the type of mating system (table A4). For this analysis, we had to make our phylogeny ultrametric using the function compute.brlen in the package ape (Paradis et al. 2004). Next, we edited branch lengths of conspecific populations to make them one-tenth of the branch length of sister species, consistent with our analyses of breeding season length and mating system (fig. A1*c*; Nexus file in part 1 of the additional supplements).

To investigate whether the expression of resource defense polygyny was associated with stronger degrees of sexual dimorphism, we used generalized mixed effects models with the fixed effect of mating system type (scramble competition or resource defense). The response variable was our sexual dimorphism index, and consistent with the nature of this index, we used a zero-inflated Poisson error distribution in our models, fit through a Bayesian approach implemented in the package MCMCglmm (Hadfield 2010*b*) in R, version 3.1.3 (R Development Core Team 2015). According to this approach, the structure of the phylogenies is expressed in a relatedness matrix A, in which element A_{ij} is the amount of time elapsed since the common ancestor of the whole phylogeny (time root of the tree) until the last common ancestor of taxa *i* and *j*. This relatedness matrix is then used as the covariance structure for the random effect of the terminal taxa in our phylogeny. We set up our priors as list (R = list (V = diag (2), nu = 0.002, fix = 2), G = list (G1 = list (V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000))), using parameter expansion for the phylogeny prior, following Hadfield (2010*a*). We ran three simultaneous Markov chain Monte Carlo (MCMC) chains for 5 million iterations, with a burn-in period of 4 million iterations, after which the chains were sampled every 1,000th iteration. Convergence of the chains were checked with Gelman and Rubin's (1992) convergence diagnostic, and we also checked the chains for autocorrelation with the function autocorr in the package coda (Plummer et al. 2006). The scripts of the analyses can be found in part 2 of the additional supplements.

The 95% highest posterior density interval of the effect of mating system on sexual dimorphism included only positive values in the three simultaneous MCMC chains that we ran (0.57–1.78, 0.59–1.74, and 0.52–1.69). This result indicates that higher degrees of sexual dimorphism were associated with resource defense polygyny (median = 4, range = 0–6), rather than with scramble competition (median = 1, range = 0–4; fig. 4).

The causal link between the length of breeding season and the type of mating system has been rarely explored in any animal group, and our results clearly show that scramble competition polygyny is prevalent in harvestman species that experience short breeding seasons, whereas re-

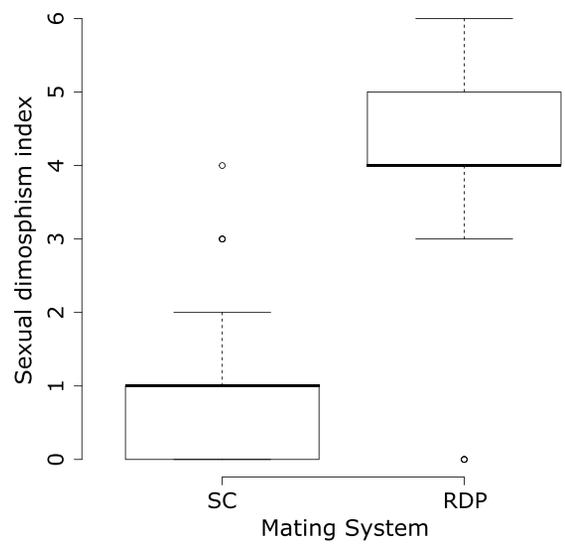

Figure 4: Higher degrees of sexual dimorphism (measured by our sexual dimorphism index; see text for details) in the harvestmen are associated with resource defense mating systems (RDP), in comparison with scramble competition mating systems (SC). Boldface horizontal lines represent medians, boxes represent interquartile ranges, and whiskers represent minimum and maximum values, excluding outliers. Outliers are defined as lying at more (or less) than 1.5 times the interquartile range above the upper quartile (or below the lower quartile) and are represented by open circles.

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source defense polygyny occurs mostly among species with long breeding seasons. Considering that the length of breeding season seems to be directly influenced by abiotic factors (fig. 2), such as temperature and precipitation, there is an indirect link between climatic conditions and the type of mating system. The type of mating system, in turn, has an effect on the degree of sexual dimorphism in body structures related to male-male fights. As should be expected, species or populations exhibiting resource defense were more sexually dimorphic than species exhibiting scramble competition. Assuming that the intensity of sexual selection on males is stronger in resource defense polygyny than in scramble competition polygyny (Emlen and Oring 1977; Shuster and Wade 2003), we have a putative answer to the question raised in the beginning of this article. Taken together, the results reported here suggest that sexual selection may be stronger in regions with hot-humid conditions (i.e., tropical climate), where long breeding seasons favor resource or female defense mating systems and, consequently, high male investment in body size and weaponry. In the future, it would be important to investigate whether the patterns reported here for harvestmen also hold for other taxa, including other terrestrial arthropods and vertebrates. Furthermore, it would be interesting to test whether there is a link between environmental conditions and direct measures of the intensity of sexual selection.

Postovipositional Parental Care

Postovipositional parental care usually requires considerable adult longevity, because parents must not only survive to oviposit but also live long enough to care for one or more clutches (Tallamy and Wood 1986). All cases of postovipositional parental care in harvestmen are restricted to representatives of the suborder Laniatores, which includes nearly 4,200 species distributed mainly between the tropical lines (Kury 2012)—despite the fact that a large fraction of these species is actually found in areas climatically classified as temperate (Buzatto et al. 2013). There is little information on adult lifespan for species of this suborder, but all species studied so far live at least 1 year as adults (Gnaspini 2007). The other two most speciose suborders, Eupnoi and Dyspnoi, comprise together nearly 2,200 species, distributed mainly in temperate or cold regions (Kury 2012). In both suborders, adult lifespan is restricted to a few months, and individuals usually die soon after oviposition. In the few species that live more than 1 year, mating takes place during a restricted period (Belozerov 2012). The constraint imposed by a short lifespan makes prolonged association between parents and offspring unlikely, which may partially explain why parental care is completely absent in species of Eupnoi and Dyspnoi (Machado and Macías-Ordóñez 2007). Although most species of Laniatores probably live more than 1 year, the length of breeding season in the suborder shows great variation depending on the species and on the locality where it lives (see above). In species in which the breeding season is very short, postovipositional parental care is unlikely either because prolonged association between parents and offspring is impossible or because the marginal costs imposed on the parents are very high. Therefore, we predict that the length of breeding season among species of the suborder Laniatores will have a positive effect on the presence of postovipositional parental care.

The presence of postovipositional parental care certainly does not depend exclusively on the length of breeding season. There are several other factors that may influence the costs and benefits associated with this behavior (Alonso-Alvarez and Velando 2012). Although the costs of egg attendance in harvestmen have been quantified in only three species, there is no evidence that caring individuals have higher mortality than noncaring individuals. In one species exhibiting exclusive maternal care, the only detectable cost of egg attendance was an 18% reduction in female lifetime fecundity (Buzatto et al. 2007). In two species exhibiting exclusive paternal care, caring males have higher survival rates than noncaring males (Requena et al. 2012; Requena and Machado 2015*a*). Thus, based on what we know, it is difficult to predict how the costs of egg attendance in harvestmen will vary in broad geographic scales. However, field experiments on the benefits of egg attendance in several harvestman species indicate that the presence of the parent is crucial to prevent egg predation (references in table A5). In some of these studies, ants were among the most important egg predators, and we know that predation pressure promoted by ants and other predatory arthropods is significantly higher in tropical climates (Novotny et al. 2006). Thus, the benefits of egg attendance could be higher in hot-humid climates, where biotic interactions are likely to be more intense (Schemske et al. 2009).

There is no universally accepted proxy for biotic interactions in the macroecological literature, but here we used actual evapotranspiration (AET), which is a measure of the water-energy balance and net primary productivity (Hawkins et al. 2003; Mu et al. 2011). We selected this variable because there is some empirical evidence showing that energy availability is positively related to the abundance of ants (Kaspari et al. 2000), an important group of egg predator in harvestmen (Machado and Macías-Ordóñez 2007). Moreover, there are meta-analytical studies on the global scale showing that energy availability is also positively related to species richness in many different taxa (Field et al. 2009) and to the intensity of egg predation on unattended clutches of terrestrial arthropod species (Santos et al., forthcoming). Therefore, assuming that AET is a good proxy for the intensity of biotic interactions, we predict that, in all harvestman species whose length of breeding season allows long-term as-

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sociations between parents and offspring, the presence of postovipositional parental care would be positively influenced by AET.

Based on the above reasoning, we tested the idea that the probability that a species will present parental care will depend on the length of its breeding season (as a proportion of the year) and on AET. Although the evolution of exclusive maternal and paternal care in arthropods may be favored by different selective pressures (Requena et al. 2013), there is experimental evidence showing that males and females provide similar benefits to offspring in terms of protection against natural enemies (Requena et al. 2009; Gilbert et al. 2010). Therefore, we pooled together the two types of parental care in the analyses described below.

We tested our predictions with phylogenetic comparative methods, in the same way as described for the analysis of the type of mating system. In this analysis, however, we used the coordinates of each studied species to retrieve information on AET from 2000 to 2013 (available at http://modis.gsfc.nasa.gov/) for each locality using the Extract Data tool from ArcGIS software (http://www.esri.com). We gathered information on presence/absence of egg attendance for 105 species of the suborder Laniatores, but there was information on the length of breeding for only 56 of these species. Our final data set includes representatives of nine families distributed across the Americas, Europe, Asia, and Oceania. For one of the species, we found information on two different populations, leading to 57 populations (table A5). We inferred the phylogenetic relationship among species based on several molecular and morphological phylogenies (fig. A1*d*; Nexus file in part 1 of the additional supplements), setting all branch lengths to 1, except for the two populations of *Vonones sayi* (branch lengths set to 0.1). We used polytomies to indicate a lack of information when phylogenies disagreed in relation to the position of a given taxon. Finally, we checked the impact of branch lengths for the two populations of *V. sayi* on our results by reanalyzing the data with these branches set to lengths of 1, 0.01, or 0.001. Because the patterns obtained with all branch lengths were qualitatively the same (data not shown), we present only the results regarding between-population branch length = 0.1. The scripts of the analyses can be found in part 2 of the additional supplements.

Consistently with our previous analysis on the length of breeding season, we first standardized our variables to the same scale and used model selection to analyze their influence on the probability that a species would present postovipositional parental care. We built a set of candidate models that included a null model, three models with every possible combination of the fixed effects (length of breeding season and AET), and the fully parameterized model that included both fixed effects and their interaction. We then ranked the five models on the basis of their AICc and checked the best model for multicollinearity using the function corvif (Zuur et al. 2009) and for overdispersion by dividing the model's residual deviance by its residual degrees of freedom. This time we fit all models with phylogenetic logistic regression as implemented in the function phyloglm from the package phylolm (Ho and Ané 2014) in R, version 3.1.3 (R Development Core Team 2015).

The most likely model included only the proportion of the year when the species is reproductively active (table 2; ΔAICc = 2.17 with the next most likely model). As expected, the length of breeding season positively influenced the probability that a species would present postovipositional parental care (fig. 5). There was no effect of AET, which was our proxy for biotic interactions and predation pressure. The level of phylogenetic dependence on postovipositional parental care probability was estimated to be 0.19. This finding indicates that postovipositional parental care in species of the suborder Laniatores is evolutionarily more labile than the length of their breeding seasons but less labile than their mating system types (see above).

Our results show that longer breeding seasons indeed favor long-term associations between parents and offspring in harvestmen, a group in which paternal and maternal egg attendance has evolved many times independently (Machado and Macías-Ordóñez 2007). At first, it may be hard to disentangle the effect of the length of breeding season

Table 2: Model selection for the effects of actual evapotranspiration (AET) and length of breeding season (LBS) on the probability of parental care in 56 harvestman species belonging to the suborder Laniatores

Fixed effects	Log likelihood	k	AICc	ΔAICc	AIC weights	Cumulative weights
LBS	**−28.38**	**2**	**62.98**	**…**	**.60**	**.60**
LBS + AET	−28.35	3	65.14	2.17	.20	.81
LBS + AET + LBS:AET	−27.77	4	66.31	3.34	.11	.92
Null (intercept only)	−31.76	1	67.58	4.60	.06	.98
AET	−31.74	2	69.70	6.72	.02	1.00

Note: Log likelihood = the natural logarithm of the maximum likelihood; k = the number of estimable parameters; ΔAICc = the difference between the corrected Akaike information criterion (AICc) of each model and the AICc of the first model; AIC weights = the Akaike weights of each model; cumulative weights = the cumulative Akaike weights of each model and the models above it. Models are ranked by increasing AICc values, and the minimal most likely model is indicated in boldface. All models were fit with phylogenetic logistic regression.

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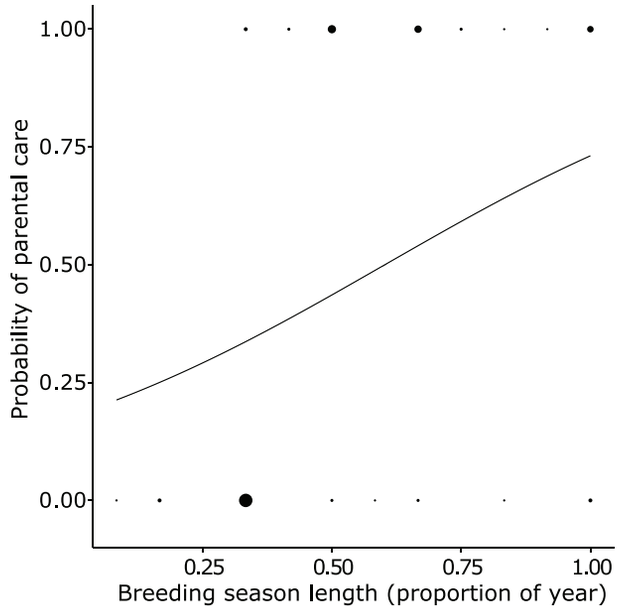

Figure 5: Probability that a harvestman species will present parental care is positively influenced by the proportion of the year adults are reproductively active (length of breeding season). The curve represents the predicted values from the minimal most likely model (see table 2), and the size of the closed circles is proportional to the number of species in each combination of parental care and length of breeding season.

from the effect of adult longevity on the probability that a species will present parental care. However, in representatives of the suborder Laniatores, adult longevity is usually much longer (Gnaspini 2007) than their breeding seasons (the mean in our data set was 4.9 months), so that longevity clearly does not constrain the evolution of parental care in this group. Moreover, we could not find evidence that predation intensity, at least our proxy for it, had an effect on the presence of parental care in harvestmen. This result, however, hardly rules out the possibility that predation plays an important role in the evolution or maintenance of parental care. First, we highlight the challenge of using, or obtaining, more direct proxies of the intensity of biotic interactions (Morales-Castilla et al. 2015). In our case, for instance, direct estimates of conspecific and ant abundances in each locality would have been more informative. Moreover, once we know that the length of breeding season is predicted by climatic variables related to temperature and precipitation (fig. 2) and that the length of breeding season predicts occurrence of parental care (fig. 5), such climatic variables should also predict parental care, as previously found by Buzatto et al. (2013). Nevertheless, we must be careful not to use such variables as proxies for predation intensity to avoid redundancy. Second, although intense predation on eggs might have been a major force favoring the evolution of postovipositional parental care in arthropods (Wilson 1975), it clearly does not explain why egg attendance has evolved in some species but not in others. Several species in our data set occur in southeastern Brazil, and there is a single locality where 11 species of the family Gonyleptidae are found together, sometimes laying eggs in the same substrate. Among these species sharing the same climatic conditions, three cover their eggs with debris and show no postovipositional parental care, four show maternal egg attendance, and four show paternal egg attendance (table A5).

Concluding Remarks

Rainfall seasonality may be found in regions along a wide range of (mean) temperatures, and the interaction between warm temperatures with pulses of precipitation in each locality defines the period of activity of many species, the temporal and spatial patterns of resource availability, and the intensity of parasites, predators, and competitors. All these factors shape or constrain reproductive traits, such as gamete production, mate search, expression of costly ornaments, and the costs and benefits of postovipositional parental care, to name a few. Thus, there is a likely causal link between climatic conditions and the expression of reproductive traits that allows us to generate predictions on how these traits vary in large geographic scales (Macías-Ordóñez et al. 2013). Here we formalized this macroecological framework, presented some general predictions focused mainly on arthropods, and explored empirical examples using harvestmen as study organisms.

Our results show that the length of breeding season in harvestmen is predicted by the number of warm months during the year and that precipitation plays a secondary role in modulating the period adults devote to reproductive activities. In turn, the length of breeding season predicts two key components of mating systems: the strategy of mate acquisition (scramble competition versus resource defense) and the presence of postovipositional parental care. Furthermore, the strategy of mate acquisition is associated with the degree of sexual dimorphism, suggesting a causal link between the intensity of sexual selection and the divergence in sexually selected traits in males. Taken together, these findings indicate that climate indeed has direct and indirect effects on sexually reproductive traits and that it is possible to derive macroecological predictions on how these traits vary in broad geographic scales in response to temperature and precipitation.

Our major challenge when approaching environmental variables from a macroecological perspective was to select potentially informative, nonredundant variables considering the physiological, ecological, and life-history traits of our study organisms. Choosing a proxy for the intensity of biotic interactions was particularly challenging, and we hope

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that the macroecological framework presented here stimulates more discussion on this subject. Another point that deserves further discussion is the procedure of measuring current climate and using that to test evolutionary hypotheses for how past climate may have shaped behavioral and morphological traits. Overall, this framework assumes relatively fast evolutionary responses to changes in climate, especially in terms of behavioral traits. In support of this view, mating strategies are known to be flexible not only between populations (examples in Thornhill and Alcock 1983) but also within the same population over the course of the breeding season (Buzatto and Machado 2008). Furthermore, the low values of phylogenetic dependence we found for the strategy of mate acquisition and presence of postovipositional parental care further support the flexibility of these traits in harvestmen. In other words, using environmental data gathered over the past five decades, we probably captured the environmental pressures that may have shaped the observed reproductive traits.

For many years, the study of reproductive strategies and sexual selection has been mostly focused on single species or populations. The advent of comparative methods in the 1980s expanded our comprehension of the evolution of morphological and behavioral traits and provided a solid analytical framework to test adaptive hypotheses in a phylogenetic context (Nunn 2011). More recently, large and detailed databases of temperature and precipitation have become available, probably stimulated by recent interest in global climate changes. Finally, the internet improved access to scientific information generated by researchers all over the world, so that the compilation of basic data on a large number of species has been greatly facilitated. We argue that the combination of these three isolated events created the unique historical opportunity to test macroecological predictions related to large-scale variation in reproductive traits. Our empirical examples with harvestmen clearly illustrate this point. Our comparative approach was possible only because we had access to (i) comprehensive phylogenies of the group, (ii) the most recent and complete data sets on climatic variables, including evapotranspiration at a global scale, and (iii) detailed information on the reproductive biology for a comprehensive set of species published in many articles in at least six different languages. Moreover, we must highlight the fact that basic information on physiology and life history was available for several species, which allowed us to strengthen the predictive power of our macroecological predictions. Considering that many other taxonomic groups are better studied than harvestmen, we are confident that the macroecological framework presented here can be successfully used to test interesting predictions about large-scale variation in reproductive traits. Although some attempts have already been conducted with birds, we expect that this article inspires future studies on other animal and plant groups for which abundant studies on reproductive traits are available in the literature.

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Literature Cited

Alonso-Alvarez, C., and A. Velando. 2012. Benefits and costs of parental care. Pages 40–61 *in* N. J. Royle, P. T. Smiseth, and M. Kölliker, eds. The evolution of parental care. Oxford University Press, Oxford.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Arnold, K. E., and I. P. F. Owens. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. Proceedings of the Royal Society B: Biological Sciences 265:739–745.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

Baeta, R., B. Faivre, S. Motreuil, M. Gaillard, and J. Moreau. 2008. Carotenoid trade-off between parasitic resistance and sexual display: an experimental study in the blackbird (*Turdus merula*). Proceedings of the Royal Society B: Biological Sciences 275:427-434.

Belozerov, V. N. 2012. Dormant stages and their participation in adjustment and regulation of life cycles of harvestmen (Arachnida, Opiliones). Entomological Review 92:688–713.

Blount, J. D., N. B. Metcalfe, T. R. Birkhead, and P. F. Surai. 2003. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. Science 300:125–127.

Bradshaw, S. D. 2003. Vertebrate ecophysiology: an introduction to its principles and applications. Cambridge University Press, New York.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Buzatto, B. A., and G. Machado. 2008. Resource defense polygyny shifts to female defense polygyny over the course of the reproductive season of a Neotropical harvestman. Behavioral Ecology and Sociobiology 63:85–94.

———. 2014. Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). Behavioural Processes 109:2–13.

Buzatto, B. A., R. Macías-Ordóñez, and G. Machado. 2013. Macroecology of harvestman mating systems. Pages 115–162 *in* R. H.

This content downloaded from 134.117.010.200 on July 24, 2016 15:32:22 PM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

Macedo and G. Machado, eds. Sexual selection: perspectives and models from the Neotropics. Elsevier, Amsterdam.

Buzatto, B. A., G. S. Requena, E. G. Martins, and G. Machado. 2007. Effects of maternal care on the lifetime reproductive success of females in a Neotropical harvestman. Journal of Animal Ecology 76:937–945.

Buzatto, B. A., J. L. Tomkins, L. W. Simmons, and G. Machado. 2014. Correlated evolution of sexual dimorphism and male dimorphism in a clade of Neotropical harvestmen. Evolution 68:1671–1686.

Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? Journal of Animal Ecology 71:79–87.

Chown, S., and S. W. Nicolson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford University Press, Oxford.

Clotfelter, E. D., D. R. Ardia, and K. J. McGraw. 2007. Red fish, blue fish: trade-offs between pigmentation and immunity in *Betta splendens*. Behavioral Ecology 18:1139–1145.

Cokendopher, J. C., and S. R. Jones. 1991. Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (Simon) (Opiliones, Cosmetidae). Proceedings of the Entomological Society of Washington 93:86–91.

Conover, D. 1992. Seasonality and the scheduling of life history at different latitudes. Journal of Fish Biology 41:161–178.

Cooper, C. B., W. M. Hochachka, G. Butcher, and A. A. Dhondt. 2005. Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. Ecology 86:2018–2031.

Corbet, P. S., S. Frank, and D. Soendgerath. 2006. Voltinism of Odonata: a review. International Journal of Odonatology 9:1–44.

Curtis, D. J., and G. Machado. 2007. Ecology. Pages 280–308 *in* R. Pinto-da-Rocha, G. Machado, and G. Giribet, eds. Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge, MA.

Dale, J., C. J. Dey, K. Delhey, B. Kempenaers, and M. Valcu. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature 527:367–370.

Darlington, P. J. 1958. Area, climate and evolution. Evolution 13:488–510.

Darwin, C. 1871. The descent of man, and selection in relation to sex. J. Murray, London.

Ebensperger, L. A., D. S. Rivera, and L. D. Hayes. 2012. Direct fitness of group living mammals varies with breeding strategy, climate and fitness estimates. Journal of Animal Ecology 81:1013–1023.

Edgar, A. L. 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). Pages 1–64 *in* Miscellaneous Publications 144. Museum of Zoology, University of Michigan, Ann Arbor.

Emlen, D. J. 2008. The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics 39:387–413.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and evolution of mating systems. Science 197:215–223.

Fairbairn, D. J. 2007. Introduction: the enigma of sexual size dimorphism. Pages 1–10 *in* D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, eds. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.

Fairbairn, D. J., W. U. Blanckenhorn, and T. Székely. 2007. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.

Field, R., B. A. Hawkins, H. V. Cornell, D. J. Currie, J. A. F. Diniz-Filho, J. F. Guégan, D. M. Kaufman, et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography 36:132–147.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

Gaston, K., and T. Blackburn. 2000. Pattern and process in macroecology. Blackwell Science, Oxford.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gelman, A., and D. B. Rubin 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Gilbert, J. D. J., L. K. Thomas, and A. Manica. 2010. Quantifying the benefits and costs of parental care in assassin bugs. Ecological Entomology 35:639–651.

Gnaspini, P. 2007. Development. Pages 455–472 *in* R. Pinto-da-Rocha, G. Machado, and G. Giribet, eds. Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge, MA.

Gomez-Mestre, I., R. A. Pyron, and J. J. Wiens. 2012. Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frog. Evolution 66:3687–3700.

Grant, J. W. A., M. J. Bryant, and C. E. Soos. 1995. Operational sex ratio, mediated by synchrony of female arrival, alters the variance of male mating success in Japanese medaka. Animal Behaviour 49: 367–375.

Hadfield, J. D. 2010*a*. MCMCglmm course notes. http://cran.r-project.org/web/packages/MCMCglmm/index.html.

———. 2010*b*. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Harshman, L. G., and A. J. Zera. 2007. The cost of reproduction: the devil in the details. Trends in Ecology and Evolution 22:80–86.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, F. J. Guegan, D. M. Kaufman, J. T. Kerr, et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hebling-Beraldo, M. J., and E. G. Mendes. 1982. Tolerance to vapour pressure deficits and thermal preferences in *Discocyrtus pectinifemur* Mello-Leitão, 1937 (Opiliones, Gonyleptidae). Boletim de Fisiologia Animal da Universidade de São Paulo 5:57–71.

Ho, L. S. T., and C. Ané. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology 63:397–408.

Ims, R. A. 1988. The potential for sexual selection in males: effect of sex ratio and spatiotemporal distribution of receptive females. Evolutionary Ecology 2:338–352.

Ives, A. R., and T. Garland Jr. 2010. Phylogenetic logistic regression for binary dependent variables. Systematic Biology 59:9–26.

Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS Biology 6:e303.

Kaspari, M., L. Alonso, and S. O'Donnell. 2000. Three energy variables predict ant abundance at a geographical scale. Proceedings of the Royal Society B: Biological Sciences 267:485–489.

Kury, A. B. 2012. A synopsis of catalogs and checklists of harvestmen (Arachnida, Opiliones). Zootaxa 3184:35–58.

Lawniczak, M. K., A. I. Barnes, J. R. Linklater, J. M. Boone, S. Wigby, and T. Chapman. 2007. Mating and immunity in invertebrates. Trends in Ecology and Evolution 22:48–55.

Lawson, A. M., and J. T. Weir. 2014. Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. Ecology Letters 17:1427–1436.

Leirikh, A. N., E. N. Meshcheryakova, G. V. Kuzminykh, and D. K. Kurenshchikov. 2009. Cold hardiness and development rate as elements of adaptive strategies of phalangiid harvestmen (Opiliones,

This content downloaded from 134.117.010.200 on July 24, 2016 15:32:22 PM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

Phalangiidae) in northeastern Asia. Entomological Review 89:323–331.

Machado, G., and R. Macías-Ordóñez. 2007. Reproduction. Pages 414–454 *in* R. Pinto-da-Rocha, G. Machado, and G. Giribet, eds. Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge, MA.

Machado, G., R. Pinto-da-Rocha, and G. Giribet. 2007. What are harvestmen? Pages 1–13 *in* R. Pinto-da-Rocha, G. Machado, and G. Giribet, eds. Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge, MA.

Machado, G., and R. L. G. Raimundo. 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida: Opiliones). Ethology, Ecology and Evolution 13:133–150.

Machado, G., G. S. Requena, C. Toscano-Gadea, E. Stanley, and R. Macías-Ordóñez. 2015. Male and female mate choice in harvestmen: general patterns and inferences on the underlying processes. Pages 169-201 *in* A. V. Peretti and A. Aisenberg, eds. Cryptic female choice in arthropods: patterns, mechanisms and prospects. Springer, Switzerland.

Macías-Ordóñez, R., G. Machado, and R. H. F. Macedo. 2013. Macroecology of sexual selection: large-scale influence of climate on sexually selected traits. Pages 1–32 *in* R. H. Macedo and G. Machado, eds. Sexual selection: perspectives and models from the Neotropics. Elsevier, Amsterdam.

Magrath, M. J. L., and J. Komdeur. 2003. Is male care compromised by additional mating opportunity? Trends in Ecology and Evolution 18:424–430.

Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. Science 287:1482–1485.

McGraw, K. J., and D. R. Ardia. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. American Naturalist 162:704–712.

Morales-Castilla, I., M. G. Matias, D. Gravel, and M. B. Araújo. 2015. Inferring biotic interactions from proxies. Trends in Ecology and Evolution 30:347–356.

Moya-Laraño, J. 2010. Can temperature and water availability contribute to the maintenance of latitudinal diversity by increasing the rate of biotic interactions? Open Ecology Journal 3:1–13.

Moya-Laraño, J., M. E. T. El-Sayyid, and C. W. Fox. 2007. Smaller beetles are better scramble competitors at cooler temperatures. Biology Letters 3:475–478.

Mu, Q., M. Zhao, and S. W. Running. 2011. Improvements to a MODIS global terrestrial evapotranspiration algorithm. Remote Sensing of Environment 115:1781–1800.

Novak, T., S. Lipovšek, L. Senčič, M. A. Pabst, and F. Janžekovič. 2004. Adaptations in phalangiid harvestmen *Gyas annulatus* and *Gyas titanus* to their preferred water current adjacent habitats. Acta Oecologica 26:45–53.

Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313:1115–1118.

Nunn, C. 2011. The comparative approach in evolutionary anthropology and biology. University of Chicago Press, Chicago.

Olson, V. A., and I. P. F. Owens. 1998. Costly sexual signals: are carotenoids rare, risky or required? Trends in Ecology and Evolution 13:510–514.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, and W. Pearse. 2013. caper: comparative analyses of phylogenetics and evolution in R. R package, version 0.5. http://cran.r-project.org/package=caper.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Peel, M. C., B. L. Finlayson, and T. A. McMahon. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11:1633–1644.

Peixoto, P. E. C., A. M. Medina, and L. Mendoza-Cuenca. 2014. Do territorial butterflies show a macroecological fighting pattern in response to environmental stability? Behavioural Processes 109: 14–20.

Pienaar, J., A. Ilany, E. Geffen, and Y. Yom-Tov. 2013. Macroevolution of life-history traits in passerine birds: adaptation and phylogenetic inertia. Ecology Letters 16:571–576.

Pintor, A. F. V., L. Schwarzkopf, and A. K. Krockenberger. 2015. Rapoport's rule: do climatic variability gradients shape range extent? Ecological Monographs 85:643–659.

Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6:7–11.

Punzo, F., C. Farmer, and L. Dunham. 2007. Responses to temperature and relative humidity in the harvestman *Vonones ornatus* (Say) (Arachnida, Opiliones, Cosmetidae). Bulletin of the British Arachnological Society 14:17–21.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.r-project.org/.

Requena, G. S., B. A. Buzatto, E. G. Martins, and G. Machado. 2012. Paternal care decreases foraging activity and body condition, but does not impose survival costs to caring males in a Neotropical arachnid. PLoS ONE 7:e46701.

Requena, G. S., B. A. Buzatto, R. Munguía-Steyer, and G. Machado. 2009. Efficiency of uniparental male and female care against egg predators in two closely related syntopic harvestmen. Animal Behaviour 78:1169–1176.

Requena, G. S., and G. Machado. 2015*a*. Lack of costs associated with nest-related behaviors in an arachnid with exclusive paternal care. Oikos 124:372–380.

Requena, G. S., R. Munguía-Steyer, and G. Machado. 2013. Paternal care and sexual selection in arthropods. Pages 115–162 *in* R. H. Macedo and G. Machado, eds. Sexual selection: perspectives and models from the Neotropics. Elsevier, Amsterdam.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38–49.

———. 2000. Lack, Skutch, and Moreau: the early development of life history thinking. Condor 102:3–8.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities—historical and geographical perspectives. University of Chicago Press, Chicago.

Ricklefs, R. E., and M. Wikelski. 2002. The physiology/life-history nexus. Trends in Ecology and Evolution 17:462–468.

Roff, D. A. 2002. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Santos, F. H. 2007. Ecophysiology. Pages 473–488 *in* R. Pinto-da-Rocha, G. Machado, and G. Giribet, eds. Harvestmen: the biology of Opiliones. Harvard University Press, Cambridge, MA.

Santos, E. A. S., P. P. Bueno, J. D. J. Gilbert, and G. Machado. Forthcoming. Macroecology of parental care in arthropods: higher mortality risk leads to higher benefits of offspring protection in tropical climates. Biological Reviews.

This content downloaded from 134.117.010.200 on July 24, 2016 15:32:22 PM
All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology and Systematics 40: 245–269.

Schmid-Hempel, P. 2005. Evolutionary ecology of insect immune defenses. Annual Review of Entomology 50:529–551.

Shuster, S. M., and M. J. Wade. 2003. Mating systems and strategies. Princeton University Press, Princeton, NJ.

Siva-Jothy, M. T. 2000. A mechanistic link between parasite resistance and expression of a sexually selected trait in a damselfly. Proceedings of the Royal Society B: Biological Sciences 267:2523–2527.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. American Naturalist 133:240–256.

Stillwell, R. C., W. U. Blanckenhorn, T. Teder, G. Davidowitz, and C. W. Fox. 2010. Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: from physiology to evolution. Annual Review of Entomology 55:227–245.

Tallamy, D. W., and W. P. Brown. 1999. Semelparity and the evolution of maternal care in insects. Animal Behaviour 57:727–730.

Tallamy, D. W., and C. Schaefer. 1997. Maternal care in the Hemiptera: ancestry, alternatives, and current adaptive value. Pages 94–115 *in* J. C. Choe and B. J. Crespi, eds. The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge.

Tallamy, D. W., and T. K. Wood. 1986. Convergence patterns in subsocial insects. Annual Review of Entomology 31:369–390.

Thomas, L. K., and A. Manica. 2003. Filial cannibalism in an assassin bug. Animal Behaviour 66:205–210.

Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, MA.

Todd, V. 1949. The habits and ecology of the British harvestmen (Arachnida, Opiliones) with special reference to those of the Oxford District. Journal of Animal Ecology 18:209–229.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Willmer, P., G. Stone, and I. Johnston. 2000. Environmental physiology of animals. Blackwell, Boston.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Belknap Press of Harvard University Press, Cambridge, MA.

Wolda, H. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics 19:1–18.

Zuk, M., and A. M. Stoehr. 2002. Immune defense and host life history. American Naturalist 160(suppl.):S9–S22.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science and Business, New York.

References Cited Only in the Online Appendixes

Acosta, L. E., F. E. Pereyra, and R. A. Pizzi. 1995. Field observation on *Pachyloidellus goliath* (Opiliones, Gonyleptidae) in Pampa de Achala, province of Córdoba. Bulletin of the British Arachnological Society 10:23–28.

Bachmann, E., and M. Schaefer. 1983*a*. Notes on the life cycle of *Phalangium opilio* (Arachnida: Opilionida). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 26:255–263.

———. 1983*b*. The Opilionid fauna of a beech wood and dry grassland on limestone (Arachnida: Opilionida). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 26:141–149.

Bishop, S. C. 1949. The function of the spur on the femur of the palpus of male, *Leiobunum calcar* (Wood) (Arachnida: Phalangida). Entomological News 60:10–11.

Brown, D. 1984. Observations on the distribution and life cycle of *Dicranopalpus ramosus* (Simon, 1909). Newsletter of the British Arachnological Society 40:7–8.

Buse, A., D. Hadley, and T. Sparks. 2001. Arthropod distribution on an alpine elevational gradient: the relationship with preferred temperature and cold tolerance. European Journal of Entomology 98:301–309.

Buzatto, B. A., G. S. Requena, R. S. Lourenço, R. Munguía-Steyer, and G. Machado. 2011. Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones). Evolutionary Ecology 25:331–349.

Caetano, D. S., and G. Machado. 2013. The ecological tale of Gonyleptidae (Arachnida, Opiliones) evolution: phylogeny of a Neotropical lineage of armored harvestmen using ecological, behavioral, and chemical characters. Cladistics 29:589–609.

Canals, J. 1936. Observaciones biológicas en arácnidos del orden Opiliones. Revista Chilena de Historia Natural 40:61–63. [In Spanish.]

Capocasale, R. M., and L. Bruno-Trezza. 1964. Biología de *Acanthopachylus aculeatus* (Kirby, 1819) (Opiliones: Pachylinae). Revista de la Sociedad Uruguaya de Entología 6:19–32. [In Spanish.]

Chelini, M. C., and G. Machado. 2012. Costs and benefits of temporary brood desertion in a Neotropical harvestman (Arachnida: Opiliones). Behavioral Ecology and Sociobiology 66:1619–1627.

Cloudsley-Thompson, J. L. 1948. Notes on Arachnida. 4. Courtship behaviour of the harvester *Mitopus morio*. Annual Magazine of Natural History 11:809–810.

Cokendolpher, J. C. 1984. Revision of the harvestman genus *Leptobunus* and dismantlement of the Leptobunidae (Arachnida: Opiliones: Palpatores). Journal of the New York Entomological Society 92:371–402.

Cokendolpher, J. C., W. P. MacKay, and M. H. Muma. 1993. Seasonal populations phenology and habitat preferences of southwestern New Mexico. Southwestern Naturalist 38:236–240.

Cokendolpher, J. C., and W. D. Sissom. 2000. Further contributions to the study of *Dalquestia* (Opiliones: Sclerosomatidae). Entomological News 111:243–249.

DaSilva, M. B., and P. Gnaspini. 2009. A systematic revision of Goniosomatinae (Arachnida: Opiliones: Gonyleptidae), with a cladistic analysis and biogeographical notes. Invertebrate Systematics 23:530–624.

de Graaf, H. W. 1882. Sur la construction des organes génitaux des Phalangiens. E. J. Brill, Leiden, Netherlands. [In French.]

Edgar, A. L. 1961. Mating and oviposition in the phalangid *Leiobunum longipes* (Arachnoidea, Opiliones). American Zoologist 1:352.

Elpino-Campos, A., W. Pereira, K. Del-Claro, and G. Machado. 2001. Behavioural repertory and notes on natural history of the Neotropical harvestman *Discocyrtus oliverioi* (Opiliones: Gonyleptidae). Bulletin of the British Arachnological Society 12:144–150.

Forster, R. R. 1954. The New Zealand harvestmen (sub-order Laniatores). Canterbury Museum Bulletin 2:1–329.

Forster, R. R., and L. Forster. 1999. Spiders of New Zealand and their worldwide kin. Otago University Press, Dunedin, New Zealand.

Freudenthaler, P. 1994. Bodenbewohnende Spinnen und Weberknechte aus der Pleschinger Sandgrube bei Linz, Oberösterreich (Arachnida: Aranei, Opiliones). Naturkdunde Jahrbücher Stadt Linz 37/39:393–427. [In German.]

———. 1999. Epigäische Spinnen und Weberknechte zweier Blockschutt-Habitate im Ranna-Tal, Oberösterreich (Arachnida: Aranea, Opiliones). Beitrage Naturkdunde Oberösterreichs 7:143–152. [In German.]

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All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

Friebe, B., and J. Adis. 1983. Entwicklungzyklen von Opiliones (Arachnida) im Schwarzwasser-Überschwemmungswald (Igapó) des Rio Tarumã Mirim (Zentralamazonien, Brasilien). Amazoniana 8:101–110. [In German.]

García-Hernández, S., and G. Machado. 2014. Eficiencia del cuidado maternal en un opilión cavernícola. Actas del IV Congresso Latinoamericano de Aracnologia, Morelia, Michoácan, Mexico. [In Spanish.]

Giribet, G., L. Vogt, A. Pérez-González, P. Sharma, and A. B. Kury. 2010. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. Cladistics 26:408–437.

Gnaspini, P. 1995. Reproduction and postembryonic development of *Goniosoma spelaeum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). Invertebrate Reproduction and Development 28:137–151.

Goodnight, C. J. 1958. Two representatives of a tropical suborder of opilionids (Arachnida) found in Indiana. Proceedings of the Indiana Academy of Science 67:322–323.

Goodnight, C. J., and M. L. Goodnight. 1976. Observations on the systematics, development and habits of *Erginulus clavotibialis* (Opiliones: Cosmetidae). Transactions of the American Microscopical Society 95:654–664.

Gruber, J. 1993. Beobachtungen zur Ökologie und Biologie von Dicranolasma scabrum (Herbst) (Arachnida: Opiliones). Teil I. Annalen des Naturhistorischen Museums in Wien 94/95B:393–426. [In German.]

———. 1996. Beobachtungen zur Ökologie und Biologe von *Dicranolasma scabrum* (Herbst, 1799) Teil II: Fortpflanzung, Entwicklung und Wachstum. Annalen des Naturhistorischen Museums in Wien 98B:71–110. [In German.]

Gueutal, J. 1944. La ponte chez un opilion: *Phalangium opilio* Linné. Revue Francaise d'Entomologie 11:6–9. [In French.]

Hara, M. R., P. Gnaspini, and G. Machado. 2003. Male guarding behavior in the Neotropical harvestman *Ampheres leucopheus* (Mello-Leitão, 1922) (Opiliones, Laniatores, Gonyleptidae). Journal of Arachnology 31:441–444.

Hedin, M., N. Tsurusaki, R. Macías-Ordóñez, and J. W. Shultz. 2012. Molecular systematics of sclerosomatid harvestmen (Opiliones, Phalangioidea, Sclerosomatidae): geography is better than taxonomy in predicting phylogeny. Molecular Phylogenetics and Evolution 62:224–236.

Hunt, G. S. 1979. Male dimorphism and geographic variation in the genus *Equitius* Simon (Arachnida, Opiliones). PhD thesis, University of New South Wales, Sydney.

Immel, V. 1955. Einige Bemerkungen zur Biologie von *Platybunus bucephalus* (Opiliones, Eupnoi). Zoologische Jahrbücher, Abteilung für Systematik 83:475–484. [In German.]

Juberthie, C. 1961. Données sur la biologie des *Ischyropsalis* C.L.K. (Opilions, Palpatores, Ischyropsalidae). Annales de Spáléologie 16: 381–395. [In French.]

———. 1964. Recherches sur la biologie des opilions. Annales de Spáléologie 19:1–244. [In French.]

———. 1972. Reproduction et développement d'un opilion Cosmetidae, *Cynorta cubana* (Banks), de Cuba. Annales de Spáléologie 27: 773–785. [In French.]

Juberthie, C., and A. Muñoz-Cuevas. 1971. Sur la ponte de *Pachylus quinamavidensis* (Opilion, Gonyleptidae). Bulletin de la Société d'Histoire Naturelle de Toulouse 107:468–474. [In French.]

Kaestner, A. 1928. Opiliones (Weberknechte, Kanker). Pages 1–51 *in* F. Dahl, ed. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. Gustav Fischer, Jena, Germany. [In German.]

Legg, G., and E. B. Pabs-Garnon. 1989. The life history of a tropical forest cyphophthalmid from Sierra Leone (Arachnida: Opiliones). Pages 222–230 *in* J. Haupt, ed. XI Europäisches Arachnologisches Colloquium. Technische Universität Berlin, Berlin.

Machado, G. 2002. Maternal care, defensive behavior, and sociality in Neotropical *Goniosoma* harvestmen (Arachnida, Opiliones). Insectes Sociaux 49:1–6.

———. 2007. Maternal or paternal egg guarding? revisiting parental care in triaenonychid harvestmen (Opiliones). Journal of Arachnology 35:202–204.

Machado, G., and P. S. Oliveira. 1998. Reproductive biology of the Neotropical harvestman *Goniosoma longipes* (Arachnida, Opiliones: Gonyleptidae): mating and oviposition behaviour, brood mortality, and parental care. Journal of Zoology 246:359–367.

———. 2002. Maternal care in the Neotropical harvestman *Bourguyia albiornata* (Arachnida, Opiliones): oviposition site selection and egg protection. Behaviour 139:1509–1524.

Machado, G., G. S. Requena, B. A. Buzatto, F. Osses, and L. M. Rossetto. 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. Sociobiology 44:577–598.

Machado, G., and J. G. Warfel. 2006. First case of maternal care in the family Cranaidae (Opiliones: Laniatores). Journal of Arachnology 34: 269–272.

Machado, S. F., R. L. Ferreira, and R. P. Martins. 2003. Aspects of the population ecology of *Goniosoma* sp. (Arachnida, Opiliones, Gonyleptidae) in limestone caves in southeastern Brazil. Tropical Zoology 16:13–31.

Macías-Ordóñez, R. 1997. The mating system of *Leiobunum vittatum* Say, 1821 (Arachnida: Opiliones: Palpatores): resource defense polygyny in the striped harvestman. PhD thesis, Lehigh University, Bethlehem, PA.

———. 2000. Touchy harvestmen. Natural History 109:58–61.

MacKay, W., C. Grimsley, and J. C. Cokendolpher. 1992. Seasonal changes in a population of desert harvestmen, *Trachyrhinus marmoratus* (Arachnida: Opiliones), from western Texas. Psyche 99: 207–213.

Matthiesen, F. A. 1975. Sobre a postura de *Discocyrtus pectinifemur* Mello-Leitão, 1937 (Opiliones, Gonyleptidae). Ciência and Cultura 35:1339–1341. [In Portuguese.]

———. 1983. Comportamento sexual de um opilião brasileiro *Discocyrtus pectinifemur* Mello-Leitão, 1937 (Opiliones: Gonyleptidae). Ciência and Cultura 35:1339–1341. [In Portuguese.]

Maury, E. A., and A. H. Roig. 1985. Triaenonychidae sudamericanos. I. El género *Ceratomontia* Roewer, 1915 (Opiliones, Laniatores). Historia Natural 5:77–92. [In Spanish.]

Meijer, J. 1972. Some data on the phenology and the activity patterns of *Nemastoma lugubre* (Müller) and *Mitostoma chrysomelas* (Herman) (Nemastomatidae: Opilionida:Arachnida). Netherlands Journal of Zoology 22:105–118.

———. 1984. Different phenological strategies in two nemastomatid harvestmen (Arachnida: Opilionida: Nemastomatidae). Bulletin of the British Arachnological Society 6:211–216.

Mendes, A. C. 2009. Avaliação do status sistemático dos táxons supragenéricos da infra-ordem Insidiatores Loman, 1902 (Arachnida, Opiliones, Laniatores). PhD thesis, Museu Nacional do Rio de Janeiro, Rio de Janeiro. [In Portuguese.]

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All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

Mestre, L. A., and R. Pinto-da-Rocha. 2004. Population dynamics of an isolated population of the harvestman *Ilhaia cuspidata* (Opiliones, Gonyleptidae) in Araucaria Forest (Curitiba, Paraná, Brazil). Journal of Arachnology 32:208–220.

Mitov, P. 1997. Preliminary observation on the spatial distribution of the harvestmen (Opiliones, Arachnida) from Vitosha Mt. (SW Bulgaria). Pages 249–258 *in* M. Zabka ed. Proceedings of the 16th European Colloquium of Arachnology. Wydawnictwo Wyzszej Szkoły Rolniczo-Pedagogicznej, Siedlce, Poland.

Miyoshi, Y. 1941. Reproduction and post-embryonic development in the Japanese laniatorid *Pseudobiantes japonicus*. Acta Arachnologica 6:98–107. [In Japanese.]

Mora, G. 1990. Parental care in a Neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). Animal Behaviour 39:582–593.

———. 1991. Site-based mating system in a tropical harvestman. PhD thesis, University of Florida, Gainesville, FL.

Nazareth, T. M., and G. Machado. 2009. Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) with description of a new and independently evolved case of paternal care in harvestmen. Journal of Arachnology 37:127–134.

———. 2010. Mating system and exclusive postzygotic paternal care in a Neotropical harvestman (Arachnida: Opiliones). Animal Behaviour 79:547–554.

Parisot, C. 1962. Étude de quelques opilions de Lorraine. Vie et Millieu 13:179–197. [In French.]

Pereira, W., A. Elpino-Campos, K. Del-Claro, and G. Machado. 2004. Behavioral repertory of the Neotropical harvestman *Ilhaia cuspidata* (Opiliones, Gonyleptidae). Journal of Arachnology 32:22–30.

Phillipson, J. 1959. The seasonal occurrence, life histories and fecundity of harvest-spiders (Phalangida, Arachnida) in the neighborhood of Durham City. Entomologist's Monthly Magazine 95:134–138.

Pinto-da-Rocha, R., C. Bragagnolo, F. P. L. Marques, and M. Antunes Jr. 2014. Phylogeny of harvestmen family Gonyleptidae inferred from a multilocus approach (Arachnida: Opiliones). Cladistics 30: 519–539.

Rambla, M. 1986. Nuevos datos sobre Dicranopalpus ramosus (Simon, 1909) (Arachnida, Opiliones, Phalangiidae). Actas del X Congreso Internacional de Aracnología, Jaca/España 1:273–282. [In Spanish.]

Ramires, E. N., and A. A. Giaretta. 1994. Maternal care in a Neotropical harvestman, *Acutisoma proximum* (Opiliones, Gonyleptidae). Journal of Arachnology 22:179–180.

Requena, G. S., and G. Machado. 2014. Mating behavior of a Neotropical arachnid with exclusive paternal care. Acta Ethologica 17:23–30.

———. 2015*b*. Effects of egg attendance on male mating success in a harvestman with exclusive paternal care. Behavioral Ecology 26: 926–935.

Rodríguez, C. A., and S. Guerrero. 1976. La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). Biotropica 8:242–247. [In Spanish.]

Rojas, A. 2013. Why would mud-nest harvestmen *Poassa limbata* (Opiliones, Manaosbiidae) take over old nests instead of constructing a new one? 50th Meeting of the Association for Tropical Biology and Conservation and Organization for Tropical Studies, June 23–27, San Jose, Costa Rica.

Santos, F. H. S. 2003. Estudo de parâmetros fisiológicos relacionados ao modo de vida cavernícola em espécies do gênero *Goniosoma* (Opiliones, Gonyleptidae). PhD thesis, University of São Paulo, São Paulo. [In Portuguese.]

Schaefer, M. 1986. Studies on the role of opilionids as predators in a beech wood ecosystem. Pages 255–260 *in* W. G. Eberhard, Y. D. Lubin, and B. C. Robinson, eds. Proceedings of the 9th International Arachnological Congress. Smithsonian Institution Press, Washington, DC.

Silva, N. F. S., and R. H. Willemart. 2015. Foraging, oviposition sites and notes on the natural history of the harvestman *Heteromitobates discolor* (Opiliones, Gonyleptidae). Biota Neotropica 15:e20140186.

Slagsvold, T. 1976. The phenology of *Mitopus morio* (Fabr.) (Opiliones) in Norway. Norwegian Journal of Entomology 23:7–16.

Stanley, E. 2011. Egg hiding in four harvestman species from Uruguay (Opiliones: Gonyleptidae). Journal of Arachnology 39:495–496.

Tischler, W. 1967. Zur Biologie und Ökologie des Opilioniden *Mitopus morio* F. Biologisches Zentralblatt 86:473–484. [In German.]

Tsurusaki, N. 2003. Phenology and biology of harvestmen in and near Sapporo, Hokkaido, Japan, with some taxonomical notes on *Nelima suzukii* n. sp. and allies (Arachnida: Opiliones). Acta Arachnologica 52:5–24.

Wijnhoven, H. 2013. Sensory structures and sexual dimorphism in the harvestman *Dicranopalpus ramosus* (Arachnida: Opiliones). Arachnologische Mitteilungen 46:27–46.

Willemart, R. H. 2001. Egg covering behavior of the Neotropical harvestman *Promitobates ornatus* (Opiliones, Gonyleptidae). Journal of Arachnology 28:249–252.

Willemart, R. H., J. P. Farine, A. V. Peretti, and P. Gnaspini. 2006. Behavioral roles of the sexually dimorphic structures in the male harvestman *Phalangium opilio* (Opiliones, Phalangiidae). Canadian Journal of Zoology 84:1763–1774.

Willemart, R. H., and P. Gnaspini. 2004. Breeding biology of the cavernicolous harvestman *Goniosoma albiscriptum* (Arachnida, Opiliones, Laniatores): sites of oviposition, egg batches characteristics and subsocial behaviour. Invertebrate Reproduction and Development 45:15–28.

Zatz, C. 2010. Seleção sexual e evolução do dimorfismo sexual em duas espécies de opiliões (Arachnida: Opiliones). Master's thesis, University of São Paulo, São Paulo. [In Portuguese.]

Zatz, C., R. M. Werneck, R. Macías-Ordóñez, and G. Machado. 2011. Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). Behavioral Ecology and Sociobiology 65:995–1005.

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