VOL. 201, NO. 3 THE AMERICAN NATURALIST MARCH 2023

SYMPOSIUM

The Geography of Sexual Conflict: A Synthetic Review*

Ryan Bacon,[1] **Dante Washington,**[1,2] **Maya-K Johnson,**[1,2] **and Mercedes Burns**[1,†]

1. Department of Biological Sciences, University of Maryland, Baltimore County, Baltimore, Maryland 21250; 2. Louis Stokes Alliance for Minority Participation Undergraduate Program, University of Maryland, Baltimore County, Baltimore, Maryland 21250

Submitted September 13, 2021; Accepted August 1, 2022; Electronically published January 24, 2023

Online enhancements: supplemental PDF.

ABSTRACT: Sexual conflict is a mechanism of selection driven by the divergent fitness interests between females and males. This disagreement can be great enough to promote antagonistic/defensive traits and behaviors. Although the existence of sexual conflict has been identified in many species, less research has explored the conditions that initially promote sexual conflict in animal mating systems. In previous work in Opiliones, we observed that morphological traits associated with sexual conflict occurred only in species from northern localities. We hypothesized that by shortening and compartmentalizing time periods optimal for reproduction, seasonality represents a geographic condition sufficient to promote sexual conflict. We conducted a systematic review of the literature on reproductive traits and behaviors. Using standardized criteria, we reviewed publications to identify whether subjects occurred in a temperate (high-seasonality) or tropical (low-seasonality) biome. After identifying and adjusting for a publication bias toward temperate research, we identified no significant difference in the strength of sexual conflict between temperate and tropical study systems. A comparison between the distribution of taxa studied in sexual conflict articles and articles focused on general biodiversity indicates that species with conflict-based mating systems more accurately represent the distribution of terrestrial animal species. These findings contribute to ongoing efforts to characterize the origins of sexual conflict as well as life history traits that covary with sexual conflict.

Keywords: sexual conflict, tropical biomes, temperate biomes, systematic review.

Introduction

Sexual conflict was first described in a 1966 book titled *Adaptation and Natural Selection* by George C. Williams. Some debate over the exact meaning of the term exists, however; for some researchers, sexual conflict describes a mechanism of selection rooted in the conflict between the different fitness interests of males and females (Parker 1979; Pizzari and Snook 2003; Arnqvist and Rowe 2005; Parker 2006; Kaneshiro 2009; Pizzari and Snook 2007; Michalczyk et al. 2011; Schärer et al. 2012). Sexual conflict is broadly categorized as inter- or intralocus, depending on the specific mechanism through which the conflict is generated (Schenkel et al. 2018). Both forms of sexual conflict arise from differences in sex-specific fitness optima: intralocus conflict is due to shared genetic architecture, while interlocus sexual conflict involves alleles at different loci (Schenkel et al. 2018). In one common example of interlocus sexual conflict, males and females "disagree" over the mating rate. The optimal mating rate of males is often higher than that of females. Females maximize their fitness by being selective with their gametic investments, and males, often unable to assess their paternity, encourage mating and ensure fertilization (Kaneshiro 2009). In this case, both sexes cannot achieve their maximum fitness simultaneously, so a mutual resolution is impossible. One possible outcome of this conflict is sexually antagonistic coevolution (Pizzari and Snook 2003; Parker 2006). Within sexually antagonistic coevolution, males and females can become locked in an arms race, each evolving traits that come at a fitness cost of the other sex (Clutton-Brock and Parker 1995; Arnqvist and Rowe 2002, 2005; Parker 2006). This can appear in the form of male traits that aid in controlling and coercing a female into mating and female defensive traits meant to avoid male coercive interactions (Clutton-Brock and Parker 1995; Arnqvist and Rowe 2002). Despite the historically mutualistic and cooperative view of reproduction, sexual conflict and sexual coercion are relatively prevalent and occur in a wide variety of species (Parker 1979; Rice 2000; Chapman et al. 2003; Arnqvist and Rowe 2005).

According to the Web of Science database, prior to 1990 fewer than five publications each year mentioned

---

* This article originated as part of the 2021 ASN Vice Presidential Symposium "The Power of Sexual Selection" and went through rigorous peer review at *The American Naturalist.*

† Corresponding author; email: burnsm@umbc.edu.

ORCIDs: Bacon, https://orcid.org/0000-0001-9361-8835; Burns, https://orcid.org/0000-0002-9450-8563.

American Naturalist, volume 201, number 3, March 2023. © 2023 The University of Chicago. All rights reserved. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/722797

the term "sexual conflict" (fig. S1). Despite 2,580 publications since 1968 mentioning or otherwise utilizing this term, interest in sexual conflict did not increase until the 1990s (Pizzari and Snook 2003; Parker 2006). This lack of attention means that many important aspects of conflict, such as the effects of different environmental pressures, are poorly understood (Pizzari and Snook 2003; Parker 2006; De Lisle et al. 2018; García-Roa et al. 2020; Plesnar-Bielak and Lukasiewicz 2021). Previous work in Opiliones, also known as harvesters or "daddy longlegs," has indicated a possible role of breeding season in the evolution of conflict (Burns et al. 2013). Features and traits specifically associated with coercive mating and interlocus sexual conflict (Burns and Shultz 2015) are restricted to temperate species of harvesters, while tropical species are almost exclusively cooperative (Burns et al. 2013). The absence of coercive mating in tropical regions and its restriction to temperate regions supports the idea that a shorter breeding season contributes to conflict. Similarly, it has been proposed that cyclical environmental changes may allow sexually antagonistic selection on loci to persist (Connallon and Hall 2016). Observations of the multiple, phylogenetically independent, and geographically organized transitions to coercive mating in temperate species of harvesters, combined with Connallon and Hall's proposal, drives the hypothesis that the length of the breeding season plays a significant role in the evolution of sexual conflict in mating systems (Burns et al. 2013). It is hypothesized that shorter breeding seasons constrain the time available to find and court a receptive mate and reproduce. This leads males to evolve coercive mating strategies. To date, relatively few studies have evaluated any connections between conflict and climate, specifically the effects of differences in the length of the breeding season (García-Roa et al. 2020).

Sexual Conflict Driven by Evolution in Phenology

Certain abiotic factors have important repercussions for the life span and activity of terrestrial animals. Colder temperatures limit their dispersal and constrain their activity (Chown and Nicholson 2004; Machado et al. 2016). In arthropods, metabolism decreases as they near the lower limit of their temperature tolerance range (Block et al. 1990). This becomes important when considering seasonality, which, in more northern latitudes, can determine the life cycle, specifically the breeding season (Zerbe et al. 2012; Machado et al. 2016). Temperate and more northerly locations that encounter high seasonality are likely to experience a shorter effective breeding season (Zerbe et al. 2012; Buzatto et al. 2013; Machado et al. 2016). Conversely, animals in southern latitudes and habitats with less seasonality are likely to experience a longer breeding season. In Opiliones, for example, previous studies that investigated a number of genera and species have identified certain factors that control the breeding season. The length of the breeding season is determined by an interaction between the number of months with appropriate levels of precipitation (humidity) and temperatures above the lower tolerable limit in Opiliones (Buzatto and Machado 2008; Buzatto et al. 2013; Machado et al. 2016). The length of the breeding season itself has been shown to positively correlate with the frequency of resource defense polygyny—a mating system in which males defend territories or resources in an attempt to control or secure mating (Buzatto and Machado 2008; Machado et al. 2016). Species of harvesters in colder areas that experience shorter breeding seasons are more likely to exhibit scramble competition polygyny, in which males do not defend females or resources (Machado et al. 2016).

While the breeding season has been shown to have a significant effect on the mating system, no studies have yet definitively connected breeding season to sexual conflict (Perry and Rowe 2018). However, sexual selection has been broadly connected to different aspects of climate and seasonality (García-Roa et al. 2020). Sexual dimorphism, a potential morphological indicator of sexual selection, has been linked to the type of mating system in harvesters (Machado et al. 2016). Harvester species with a resource defense polygyny mating system exhibited a stronger degree of sexual dimorphism, specifically those structures involved in male-male antagonistic interactions (Machado et al. 2016). The link between mating system and sexual dimorphism, combined with the correlation between mating system and breeding season length, suggests a possible connection between sexual selection and the length of the breeding season (Buzatto and Machado 2008; Machado et al. 2016). In previous work in *Nephila plumipes*, the strength and direction of selection was noted to fluctuate throughout a breeding season, highlighting the impact of seasonality on selection (Kasumovic et al. 2008).

The few studies that have investigated the specific effects of seasonality on sexual selection concluded that male-biased sexual size dimorphism was correlated with the seasonality of reproduction (Zerbe et al. 2012; Heldstab 2021). Species with a stronger seasonal component to reproductive cycles had a greater degree of male-biased sexual size dimorphism (Zerbe et al. 2012; Heldstab 2021). The proposed explanation for this trend aligns with our hypothesis in that female monopolization and male-male interactions are more likely to evolve in species with a shorter breeding season (Heldstab 2021). Female monopolization occurs in polygamous mating systems when females or resources are aggregated in such a way that defending or monopolizing them is possible (Emlen and Oring 1977). Additionally, the degree of breeding synchrony and the number of reproductive events may play a significant role in sexual dimorphism (Emlen and Oring 1977). It appears that a reduced mating season may constrain multiple animal mating systems in a similar way.

We chose to evaluate the contribution of seasonality to the strength of sexual conflict by performing a systematic review of existing reproductive research studies. A recent investigation of biodiversity publications served as inspiration for this project and the choice in methods (Titley et al. 2017). To investigate any biases in biodiversity studies between temperate and tropical regions, Titley et al. (2017) performed a meta-analysis and identified both the region that the study occurred in and the taxa studied. Taking that article as inspiration, we chose to investigate studies of sexual conflict between temperate and tropical regions. While the types of data used to establish conflict vary widely, making a true meta-analysis difficult, our aim was to provide a synthesis of the current state of sexual conflict publications and evaluate our hypothesis: if the length of the breeding season plays a significant role in the evolution of sexual conflict, then we expect sexual conflict to be more common in regions that experience high seasonality and a shorter breeding season. This would include regions experiencing a temperate climate, and we would expect that species experiencing sexual conflict in temperate regions should be more affected than those occurring in tropical regions.

Biases in Temperate Publications

To properly evaluate any differences in the effects of conflict between biomes, it is important to first evaluate any publication biases that may be present (Côté and Jennions 2013). Publication bias in ecology has received increasing research interest. An earlier ecological meta-analysis (Titley et al. 2017) suggests that there is a current research bias toward vertebrate species and temperate countries in animal biodiversity articles compared with the described proportion in taxonomic groups in animals and their geographic distribution (Mora et al. 2011). The reasoning behind this temperate bias could be attributed to the economic or political state of the countries in which these studies were performed. The number of articles on biodiversity in a country shared a positive relationship with its nominal gross domestic product (GDP; Titley et al. 2017), suggesting that the wealth of a nation heavily influences where research is done. Temperate regions may be more accessible to researchers in the Global North, and these regions are likely more familiar (Zuk 2016). In contrast, tropical countries often had few to no lead authors and averaged lower GDPs than temperate countries (Titley et al. 2017). These temperate biases, if present in studies of reproduction, could produce results that spuriously identify correlations between conflict and temperate biomes. To ensure that our results are meaningful, any bias toward temperate biomes must be accounted for in our results.

In this article, we detail the process and results of a systematic review of the reproductive biology literature spanning more than a half century of research in temperate and tropical animal systems. We use the results of this review to subsearch articles that indicate sexual conflict to be a significant mechanism in the evolution, reproductive behavior, and/or mating systems of study species. We similarly evaluate the general effect of life span and/or motility on the author-defined strength of conflict by categorically rating the life span and motility of each study species and then comparing the importance of conflict across those categories, as these variables may be important in the evolution of sexual conflict (Adler and Bonduriansky 2014; Bonduriansky 2014; Connallon 2015). While we quickly identified that the publication bias toward temperate studies swamped out any evidence of a correlation between temperate biomes and a great incidence of sexual conflict, we did discover that the distribution of taxa affected by sexual conflict mirrors the distribution of terrestrial animals. We complete the article by discussing potential experimental methods to examine the origins of sexual conflict within species or populations.

Methods

Publication Search

To evaluate any bias between temperate and tropical publications, we performed a systematic review (fig. 1). The databases Web of Science, Academic Search Ultimate, and Agricultural and Environmental Science Collection were utilized to identify academic publications. These databases were selected because they allowed the use of a single search string, and they contained the highest numbers of applicable publications. Identifying suitable publications required the creation of a specific search string that targeted studies that focused on reproductive and mating behavior in natural or wild populations. This search string eliminated unwanted topics and organisms, such as articles that dealt with maternal behavior. Maternal behavior publications were categorically eliminated because of the high proportion of articles that focused on humans. While parental investment is a source of sexual conflict, our focus is on mating system evolution, and precopulatory traits may prove to be more significant to the evolution of mating systems (Wensing et al. 2017). Furthermore, many aspects of maternal behavior are a product of, but not definitely related to, the act of mating. The search string was created through an iterative process, during which we

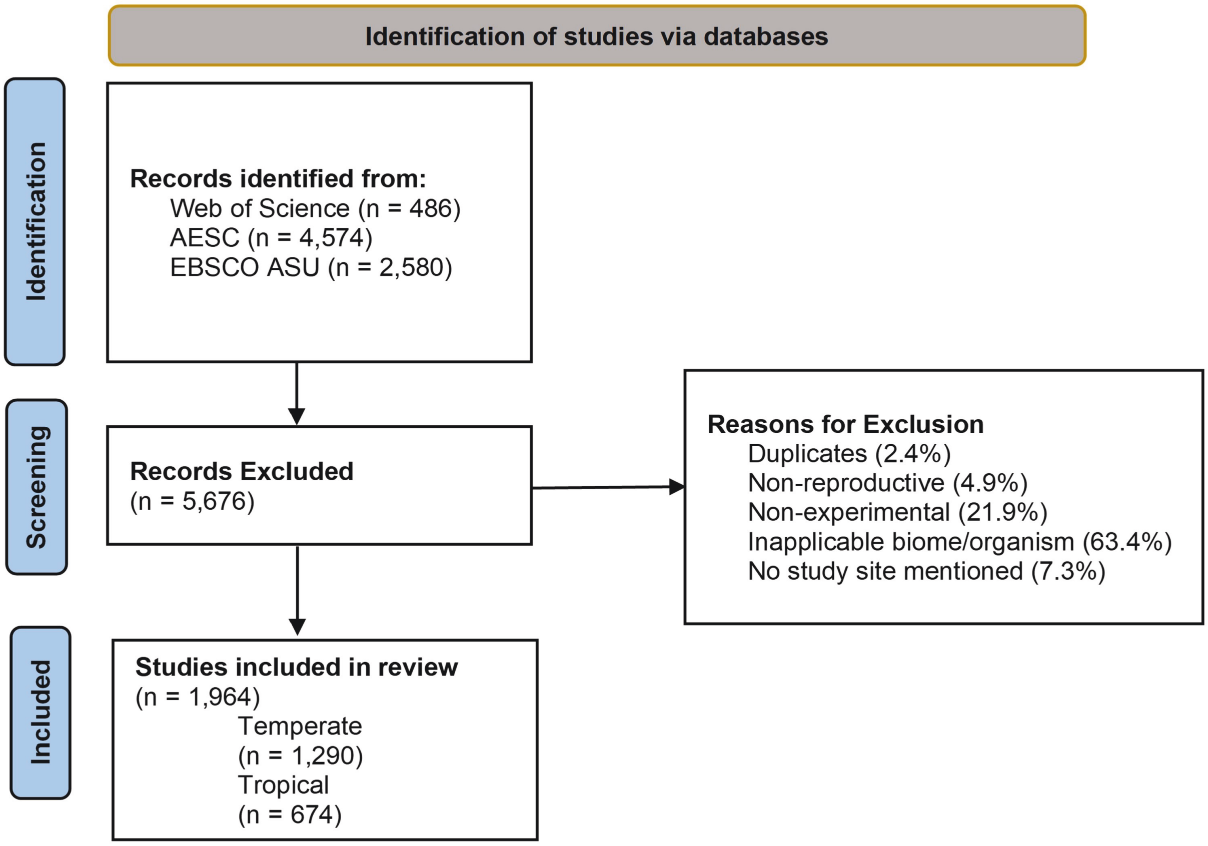


Figure 1: PRISMA diagram displaying the reasons for article rejection along with percentages based on a 100-article sample set. In total, 5,676 articles were excluded from our study, resulting in a final sample size of 1,964 articles.

identified key words and phrases from "model" publications across the three databases. Our search string was deemed complete once further revisions did not result in any appreciable decrease in the number of results across all databases.

The completed search string ("reproduct* behavior" and "mat*" and "population*" not "maternal") was then used in each of our databases. Only experimental and observational academic studies published between 1966 and January 15, 2021, were considered. The year 1966 was used because it was the year that the term "sexual conflict" was first published in an evolutionary context (Williams 1966; fig. S1). This date was selected to ensure that our sample articles were all from a time period when sexual conflict publications were also possible. The end date of January 15, 2021, represents the date at which the article search was completed and the sample articles were collected. This serves as the last possible publication date included in our study, although we cite more recent articles in this publication. Articles from our search of the three selected databases were transferred to the citation management software EndNote Online (Clarivate) for the primary and secondary reviews.

Publication Review

The articles that were analyzed were evaluated on the basis of five criteria. First, is the article an originally published observational or experimental study? If the article was not observational or experimental (i.e., a review document), it was eliminated from the set. Second, is the article reproduction focused? This included but was not limited to articles discussing sexual conflict, breeding behavior, mating calls and signals, sexual selection, and reproductive morphology. If these topics were not discussed, articles were removed from analysis. Third, does this study focus on or use wild organisms? If the organisms of study were human or entirely farm or laboratory raised for greater than three generations, the article was removed from analysis. Fourth, was the study performed in a biome of interest? Because of the complexities of assessing seasonality for arctic, desert, and marine biomes, we removed articles that focused on organisms endemic to these regions.

Fifth, does the study take place in a temperate or tropical biome (as assessed using Google Earth and a biome map from fig. 49.11 in Freeman et al. 2017)? Articles that qualified as temperate featured research in temperate forests, temperate grasslands, Mediterranean forests, temperate coniferous forests, and montane grasslands. Articles characterized as tropical included systems located in tropical wet forests, tropical dry forests, tropical coniferous forests, and tropical grasslands. Using geographic data from each article, we sorted publications into temperate and tropical subsets. Studies that focused partially in either biome of interest were retained for analysis if the other qualifying criteria were also met. In addition, studies focusing on qualifying migratory organisms were retained on the basis of where their reproduction occurred. All articles were double screened by separate reviewers to decrease bias toward our initial evaluation decisions. Each article from the temperate and tropical sets was sorted into a spreadsheet (see table S1) on the basis of their biome, to check and confirm their suitability and record their study locations, lead author institution or affiliation, and lead author location. Articles that raised questions about their suitability were evaluated by another reviewer, as were articles with outdated country information.

To identify studies implicating sexual conflict as a mechanism of importance to reproductive evolution, behavior, and/or mating system of the study species, we used the EndNote Online search option to find the term "sexual+conflict" in titles of abstracts from the reviewed temperate and tropical reproductive biology articles we had previously screened. For the purposes of this analysis, we took a broad view of sexual conflict and did not differentiate between intra- and interlocus conflict; however, we recognize that our search string and review criteria may exclude articles focused on intralocus conflict. Articles that lacked accessibility at our institution but included "sexual+conflict" in the title or abstract ($N = 2$) were requested through interlibrary loan and reviewed by R. Bacon. A total of 61 sexual conflict articles were identified. Twelve of these articles were studies of the same animal system, and four articles provided results on multiple species. In total we reviewed research on 61 total animal systems, which we also called "sexual conflict species."

To define the effect of sexual conflict on each animal system, we used the following criteria to develop a qualitative metric of sexual conflict. We ranked the importance of sexual conflict to the evolution or mating system of the species based on the authors' findings. If sexual conflict was deemed to be the most important mechanism responsible, the system was given a rank of 2. If sexual conflict was deemed to be present but other mechanisms of sexual selection were equally or more prominent to the study, a rank of 1 was made. A rank of 0 corresponded to studies where sexual conflict was discussed but no determination of its importance was given, and a rank of −1 was given for studies where sexual conflict was not found by the researchers (table S1). The sexual conflict metrics (SCMs) were averaged for temperate and tropical species and for species with multiple studies. Comparisons of sexual conflict across taxonomic differences in life span and range size were done by roughly classifying the life spans as short or long and the range sizes as small, medium, and large. As an example, arthropod life span and range size were deemed to be short and small, respectively, while avian range size was considered large.

Statistical Analyses

To evaluate publication biases between temperate and tropical studies, we compared the numbers of temperate and tropical articles within our accepted sample to previous studies of the number of described species (Mora et al. 2011) and to the number of biodiversity studies within these same regions (Titley et al. 2017). This was done using a χ^2 test. Subsequent analysis of SCMs used a weighted *t*-test approach to account for biases between temperate and tropical research. After reviewing SCMs, a Shapiro-Wilk test and subsequent nonparametric Wilcoxon rank-sum tests were used to assess normality and compare the distribution of described study species in sexual conflict publications to the described species from Titley et al. (2017).

Results

Preferred Reporting Items for Systematic Review and Meta-analysis (PRISMA)

Our initial search identified 7,640 articles, of which 1,964 were deemed appropriate for this project and were included in our statistical analyses (fig. 1). During both the initial and the secondary review process, we rejected a total of 5,676 articles. To quantify the relative frequency with which articles were rejected for the various reasons given above, we recorded the reasons and frequency of rejection from 100 of the total number of reviewed articles (fig. 1). This random sample was collected from the 7,640 articles included in our initial results. The largest percentage of rejected articles were those that investigated an inapplicable organism, such as humans or marine organisms (63.4%), and those that were nonexperimental studies, such as reviews or theoretical articles (21.9%; fig. 1). A small subset of rejected articles (7.3%) were those that did not specifically mention a study site or were otherwise inaccessible.

This subset of articles was rejected because an accurate description of the exact study or collection site was needed to assign a biome to the publication. Many countries contain both temperate and tropical regions, and it would be difficult to ascertain location from the species studied. Following the secondary review, the final accepted 1,964 articles, comprising 1,290 categorized as temperate and 674 categorized as tropical (fig. 1), were used as the sample set in which we would evaluate studies of sexual conflict.

Publication Bias Toward Temperate Reproductive Biology Articles

Following the second review of all articles, where we recorded data on the study country and first author affiliation, we compared article counts from temperate and tropical biomes to previous studies of described species (Mora et al. 2011) and biodiversity (Titley et al. 2017) in the same geographical regions. Using a χ^2 test, we found that significantly greater ($\chi^2 = 3{,}001.8$, df $= 4$, $P < .0001$) proportions of biodiversity and reproductive biological studies were performed in temperate systems compared with the proportion of animal species actually occurring in temperate regions (fig. 2). Using the location details from publications, we found that not only do reproductive studies appear to be biased toward temperate regions, but certain study (and lead author) locations appear in much higher proportions than others (figs. 3*a*, S2).

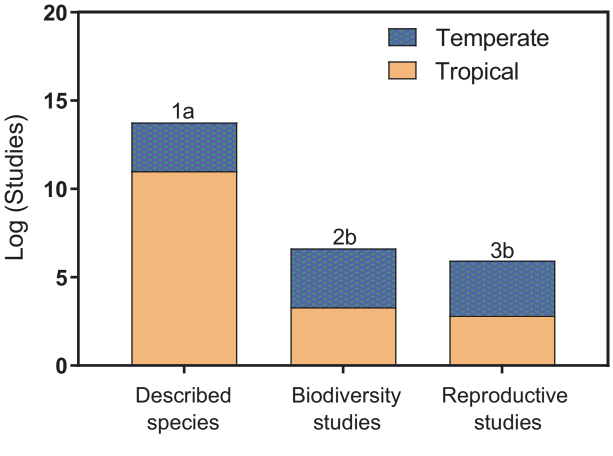


Figure 2: Geographic distribution of terrestrial species and research. The plot visualizes publication bias toward temperate research in reproductive biology. Bar 1 indicates the distribution of described terrestrial animals from Mora et al. (2011), bar 2 indicates the distribution of studies of biodiversity (Titley et al. 2017), and bar 3 shows our results for temperate and tropical studies of reproductive biology. Here, "a" indicates $P < .05$, while "b" indicates no statistically significant difference in frequency.

Sexual Conflict Publications

A total of 61 (temperate: 53; tropical: 8) sexual conflict species were identified, and we further evaluated these for author and study species location (fig. 3*b*) as well as taxonomic group (in the style of Titley et al. 2017). To account for temperate publication bias in the analysis of sexual conflict articles, we calculated weights by dividing the expected proportion of studies given random selection (0.2 for temperate, 0.8 for tropical) by the proportion of temperate and tropical reproductive biology publications we found. These weights (temperate $= 0.2/0.658$; tropical $= 0.8/0.342$) adjust the proportions of sexual conflict species found by the bias that already exists toward temperate publications and study species.

After calculating weights to properly assess any correlation between sexual conflict and geography, a weighted *t*-test revealed no statistically significant difference between adjusted SCMs of temperate and tropical species ($t = 0.72$, df $= 10.98$, $P = .487$; fig. 4). This means that after accounting for publication bias, we did not see a significantly higher SCM in temperate biomes with high seasonality. However, when comparing the proportions of sexual conflict study taxa to described terrestrial species and species diversity studied from 2011 to 2015 in Titley et al. (2017), we found that the distribution of study species from sexual conflict articles (not normally distributed following Shapiro-Wilk test: $W = 0.59$, $P < .0001$) did not significantly differ from the diversity of described terrestrial species (Wilcoxon rank-sum: $W = 52$, $P = .599$; fig. 5). Conversely, Titley et al. (2017) reported that significantly different proportions of taxa were studied in biodiversity articles compared with actual described species diversity (Wilcoxon rank-sum: $W = 24$, $P < .05$; fig. 5). Subsequent analyses failed to show a significant link between standardized metrics of sexual conflict for taxonomic group ($N = 8$; fig. 5) and average range size (small or large; Kruskal-Wallis rank sum: $\chi^2 = 3.746$, $P = .154$) or life span (i.e., short, medium, or long; $\chi^2 = 3.239$, $P = .0719$). While we took a broad view of sexual conflict, none of the articles included in this data set studied intralocus conflict. This may result from our reproductive behavior–focused search string.

Discussion

Reproductive Research Is Biased Toward Temperate Biomes

In comparing the frequency of reproductive biology studies within our results to that of animal species occurring within temperate and tropical regions, we found that temperate biomes are vastly overstudied compared with tropical regions regarding reproductive research (figs. 2–4).

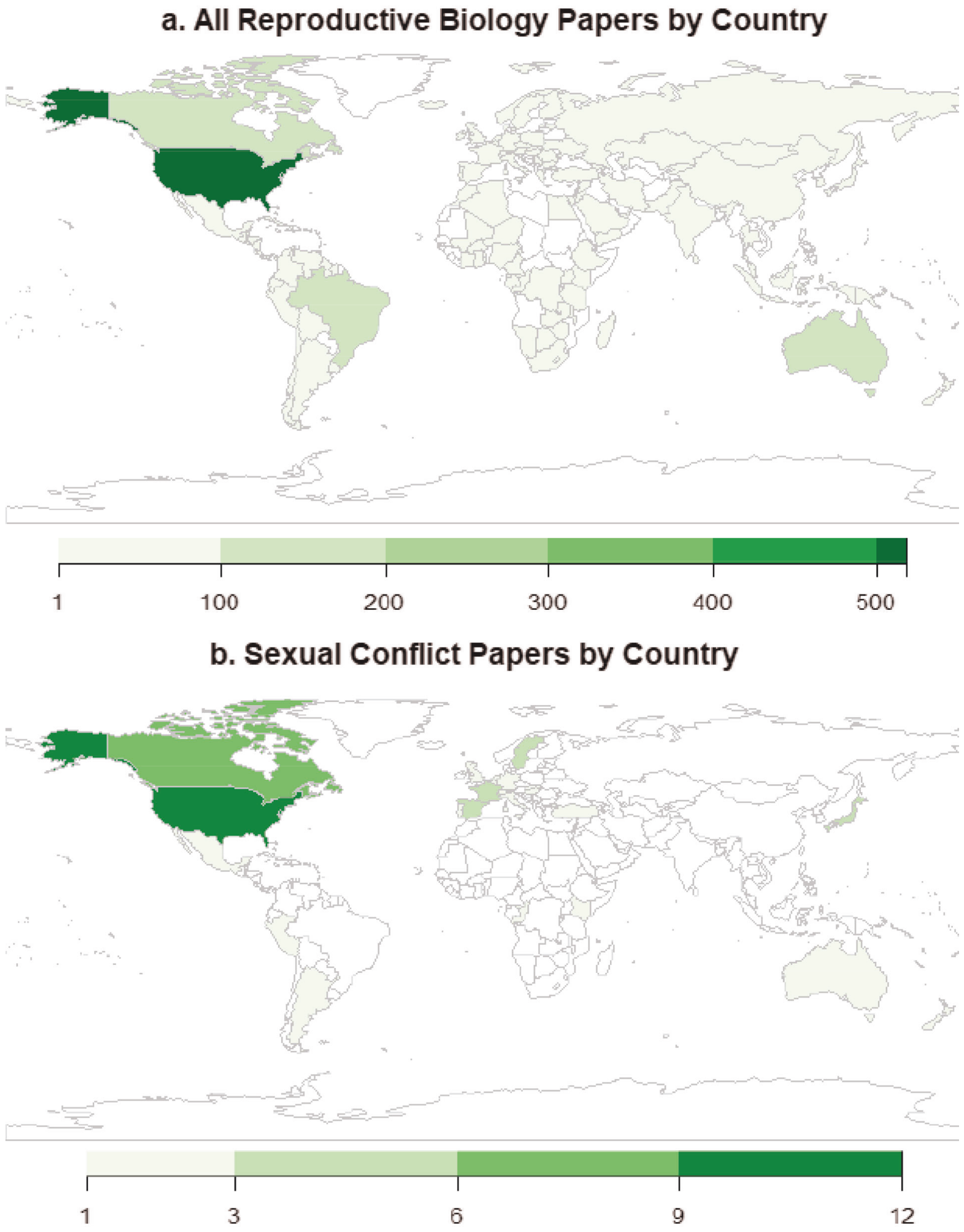


Figure 3: Global distributions of all retained reproductive biology articles (*a*) and all systems referencing sexual conflict (*b*).

Furthermore, there were a larger number of lead authors from temperate localities represented within our results; the majority of these authors resided within the United States. These results indicate that there is a strong temperate bias in biological research on reproduction (figs. 2, 4). It has been well established that a greater number of species exist within the tropics than outside of them (Corlet and Primack 2010; Mora et al. 2011; Zuk 2016). If studied according to the number of species, tropical articles should far outnumber temperate ones. However, our results corroborate what other studies have shown: a bias toward temperate regions exists in many biological research areas (Zuk 2016; Titley et al. 2017). The exact reasons for this trend are unclear; however, a few possible explanations, such as differences in GDP and a general belief that tropical regions are "different" (meaning that findings from such studies are not applicable to other systems), have been suggested (Machado et al. 2016; Zuk 2016; Titley et al. 2017).

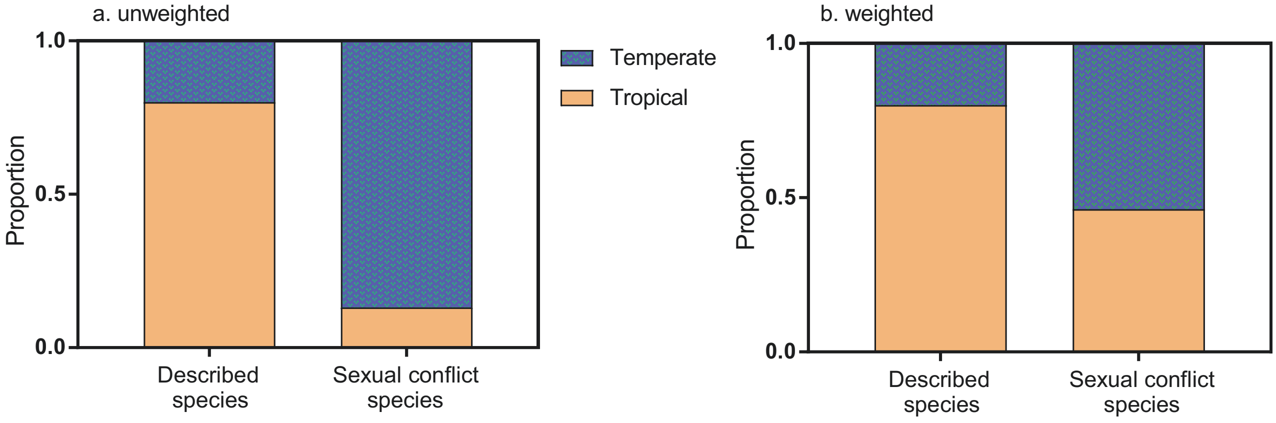


Figure 4: Proportions of described and sexual conflict species. The bar plots show sexual conflict–containing study systems before (*a*) and after (*b*) weighting the proportions of species on the basis of temperate publication bias.

A general problem with studying these regions comes from the way we delimit these areas. Researchers often mistakenly assume that "temperate" means anything nontropical and that anything between the Tropics of Cancer and Capricorn is automatically tropical (Machado et al. 2016). A wide variety of seasonality and climate patterns exists both within and outside the tropics (Machado et al. 2016). Additionally, the amount of precipitation interacts with temperature in determining the breeding season of harvesters, indicating that it is possible that the breeding season varies within a single region (Buzatto et al. 2013). Assuming that any region outside the areas between the tropics is temperate fails to consider regional abiotic differences. These regional differences make it important to sample multiple populations, even when investigations are performed within a single biome, as variations in mating system and/or sexual conflict are possible (Machado et al. 2016).

Multiple Interacting Factors May Determine the Geography of Sexual Conflict

Climate patterns and/or seasonality may represent a small part of a larger interactive network of factors that all have

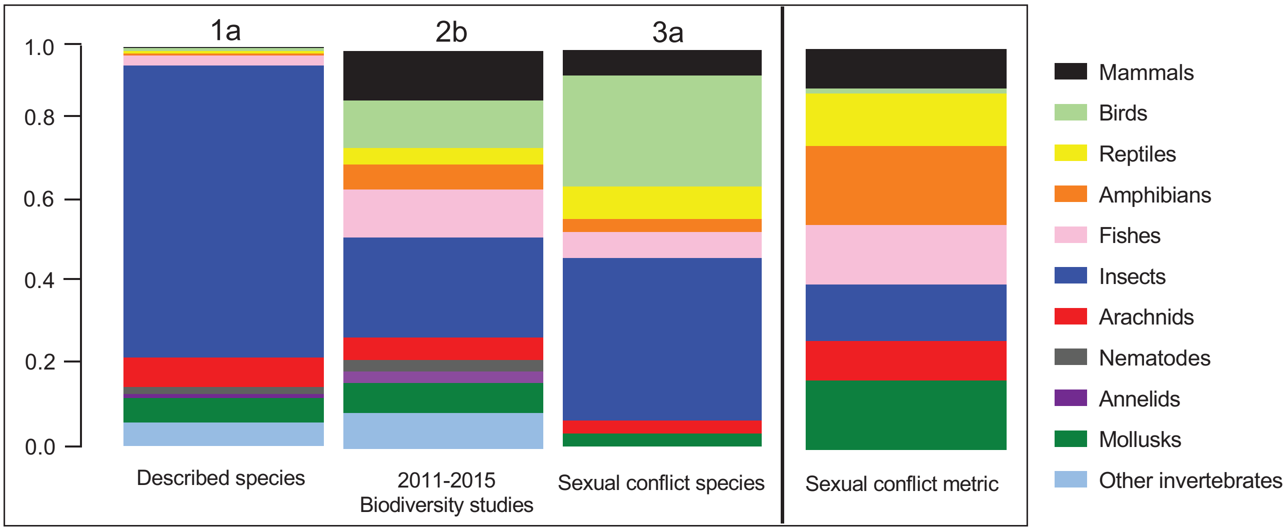


Figure 5: Proportions of species studied in three data sets. The bar plot shows described terrestrial species proportions (bar 1), species proportions from 2011–2015 biodiversity publications (bar 2; Titley et al. 2017), species proportions from sexual conflict systems in this study (bar 3), and standardized sexual conflict metric averages by taxonomic group (bar 4). Using a Wilcoxon rank-sum test for data for bars 1–3, we find that only bars 1 and 2 are significantly different ("a" represents a lack of statistical significance, while "b" represents $P < .05$).

repercussions for the strength of sexual conflict. Given the available information, we found that after accounting for the temperate bias, there was no statistically significant difference in SCMs between temperate and tropical biomes. Based on our results, this indicates that sexual conflict may not be more prevalent in temperate regions. However, this may not be the correct interpretation. As our results indicate, the amount of reproductive research does not directly correlate with species prevalence. If this were the case, temperate regions would have a much higher level of species diversity than tropical ones, reflecting the research bias indicated by our results. Moreover, the distribution of sexual conflict taxa more closely mirrors terrestrial species distributions than studies of biodiversity (fig. 5), supporting the conclusion that true species diversity, sexual conflict incidence, and the level of research are misaligned (Titley et al. 2017). This leaves the possibility that the amount of sexual conflict research in different areas does not reflect the natural occurrence of sexual conflict. Future studies, as we describe below, will need to be completed in order to reveal the true role of breeding season in the evolution of conflict.

While we propose that sexual conflict may be stronger in temperate climates because of variable seasonality, other studies have proposed opposing explanations. Increased breeding season length was shown to correlate positively with sexual selection in pipefish (Monteiro and Lyons 2012). Additionally, male harm to females was shown to be temperature dependent in *Drosophila* (García-Roa et al. 2018); specifically, less harm was noted in temperatures higher and lower than the species optimum. This result highlights the importance of temperature in determining the level of conflict, but temperature-mediated effects may vary across taxa (García-Roa et al. 2020). Other studies suggest that conflict should be weaker in stressful or otherwise less stable environments (De Lisle et al. 2018; García-Roa et al. 2020; Plesnar-Bielak and Lukasiewicz 2021), but the exact factors that make an environment stressful are likely to vary between species. De Lisle et al. (2018) additionally found the strength of sexually antagonistic selection to have a negative relationship with latitude. Together, these results suggest that conflict may actually be weaker in temperate regions than in tropical regions and that conflict may be more pronounced in more stable environments, such as those found in tropical climates, which lack seasonality (Dynessius and Jansson 2000; De Lisle et al. 2018).

Another possible explanation for a difference in conflict across climates is the spatial distribution of reproductive individuals (Machado et al. 2016; Plesnar-Bielak et al. 2020). As proposed by Machado et al. (2016), a decreased breeding season may align the reproductive interests of males and females. Populations within tropical areas are likely to include a mixture of reproductively available and unavailable females due to the extended breeding season (Machado et al. 2016). In contrast to this spatial distribution, populations within temperate areas may contain a higher number of receptive females due to the decreased time available to mate, producing alignment of male and female reproductive interests that would decrease conflict. While this does not explain the global geography of conflict, the spatial organization of receptive females may alter selection for coercive tactics, and in Opiliones it is an important factor to consider.

Breeding season may have an appreciable effect on the evolution of sexual conflict, but there are other variables that may moderate this effect. Traits such as life span and motility may mitigate the impact of a shortened breeding season. A shortened breeding season may be of increased importance for univoltine species, as they have only a singular reproductive event throughout their life span (Adler and Bonduriansky 2014). Conversely, multiple mating opportunities throughout an organism's life span—or a longer life span in general—may alter the level of sexual conflict within a population (Candolin 1998; Monteiro and Lyons 2012; Adler and Bonduriansky 2014; Bonduriansky 2014). An increased life span and number of mating opportunities may decrease the risk imposed if an organism fails to mate, and as Kasumovic et al. (2008) point out, variations in selection across a breeding season are likely to be significant in species with a shorter life span. In addition to the possible effects of life span, the ability to freely disperse throughout an environment holds the possibility to mediate local environmental effects and, as a result, sexual conflict (Eldakar et al. 2010; Connallon 2015). In water striders, females disperse away from groups with a high number of coercive males, effectively balancing out selection for increased male coercion (Eldakar et al. 2010). The importance of local adaptation and dispersal is highlighted by the fact that sexual conflict is expected to vary across a species range, being strongest near the center, where populations are more locally adapted (Connallon 2015; Connallon and Hall 2016; De Lisle 2018). Similarly, sexual conflict is expected to be strongest in populations in more heterogeneous, smaller, and/or more complex environments (Connallon 2015; Yun et al. 2017; De Lisle et al. 2018; García-Roa et al. 2018; Yun et al. 2018; Plesnar-Bielak and Lukasiewicz 2021). In light of this evidence, it is possible that motility, life span, and the number of reproductive events may mediate the level of sexual conflict imposed by a shortened breeding season.

In sum, breeding season length, local adaptation, precipitation, temperature, species range size, voltinity, motility, and environmental stress are all likely contributors to conflict (Connallon 2015; Connallon and Hall 2016; De Lisle et al. 2018; García-Roa et al. 2018; García-Roa et al.

2020). Because of the interactive nature of the multiple abiotic factors, disentangling their effects could prove difficult when evaluating the initial conditions promoting conflict.

Future Empirical Investigations Are Needed and Should Account for Interpopulation Variation

This study investigates the connection between sexual conflict and biome by evaluating the level of published conflict research within each biome. We did not detect any significant difference in SCMs; however, this review highlights a few important considerations for future research. As indicated by our review of reproductive studies, more attention needs to focus on tropical regions. Our small sample size of tropical conflict studies reflects the lack of scientific attention within these regions. In addition to increased focus on understudied regions, future investigations should sample multiple populations across the geographic range in which a species exists. Local adaptation may prove to be an important consideration for sexual conflict investigations, and sampling of single populations fails to account for any possible variation between populations. Studies investigating continuous populations spanning across regions with varied seasonality and climates would be ideal but may prove difficult. Importantly, future investigations that directly test the connection between breeding season and conflict should be completed. What follows are multiple suggested methods for evaluating the specific drivers behind the evolution of conflict in Opiliones (or other systems).

Phylogenetic Comparative Methods. While previous studies have investigated the mating systems of different harvester species within eastern North America, there are still more species for which phylogenetic and morphological comparative analyses have yet to be completed (Burns et al. 2012, 2013). North American leiobunine species were identified to be monophyletic, with female choice–based mating to be the ancestral system (Burns et al. 2012, 2013). Certain tropical Opiliones species in Central America remain unevaluated. Investigating the mating systems of these species—specifically the presence or absence of previously described coercive and cooperative suite of traits in addition to phylogenetic comparative analyses—may further support the geography of sexual conflict in Opiliones. This will further reveal the role of breeding season length in the evolution of conflict by sampling a continuum of species distributed along a latitudinal transect. If breeding season is a significant factor, then tropical species should exhibit the previously identified “cooperative” suite of traits.

Behavioral Population Crosses. One method for testing the benefits of coercive traits and strategies under a shortened breeding season is to perform transplantation experiments. In this type of study, individuals of a species ranging across temperate and tropical regions would be transplanted to a region to which they are not locally adapted. Under this design, cooperative individuals from a region with low seasonality would be transplanted into a region with high seasonality, and coercive individuals from high-seasonality regions would be transplanted to low-seasonality regions. Focal populations would be contained in outdoor enclosures that allow exposure to all of the abiotic conditions within a specific region while preventing individuals from dispersing. The fitness of these transplants (i.e., numbers of offspring, reproductive attempts, and successful reproductions) would be quantified for each region. These results would be compared with the average fitness within their home population. If coercive mating evolved as a response to a shortened breeding season, cooperative individuals (particularly males; Yun et al. 2018) transplanted from low-seasonality regions into a high-seasonality region should suffer reduced fitness. The expected explanation for this result is that they lack the coercive traits that are found in locally adapted populations. This leaves transplants suffering from a limited time to secure mating. Similarly, coercive populations transplanted from regions with a short breeding season into a region with a longer breeding season are expected to see no statistically significant change in their fecundity, although an increase may be possible. Coercive males may particularly see an increase in fitness due to the presence of coercive traits that ensure mating. The results of this experiment would support the hypothesis that coercive strategies are a local adaptation to a shortened breeding season.

Experimental Evolution. A final method of evaluating breeding season length and its effects on sexual conflict is through experimentally induced evolution trials. Previous studies have performed such trials involving sexual conflict in *Drosophila* (Hollis et al. 2019). Male *Drosophila melanogaster* have seminal fluid proteins (SFPs) that affect female mating behavior and impose a fitness cost to females (Hollis et al. 2019). Changes in these SFPs and male-female mating effects were noted to occur when monogamy was enforced over 150 generations (Hollis et al. 2019). We propose a test of the effects of the breeding season by inducing a short breeding season in experimental populations and examining the changes in SFPs, female mating behavior, and overall female survival (postmating). While other studies in *Drosophila* have indicated that temperature changes decrease conflict, none have evaluated breeding season (García-Roa et al. 2018). We suggest manipulating the length of time that males have access to females each generation. This would represent the constraint of a shortened breeding season within temperate regions but would isolate any abiotic factors, such as temperature (García-Roa et al. 2018). Results of this experiment may provide support for the explanation that seasonality limits the time available to secure mates, which imposes a selective pressure on males. This mechanism possibly drives the evolution of conflict in temperate species over tropical species.

Each of the previously mentioned methods alone may be insufficient to conclude that seasonality is a significant driver in the evolution of conflict and coercive mating. Instead, each method represents one part of an overarching objective to better understand the environmental conditions that contribute to sexual conflict. While interest in sexual conflict and sexually antagonistic selection may have increased since 1966 (fig. S1), many questions remain unanswered. These experiments aim to grant a clearer understanding of the evolution of sexual conflict.

Conclusions

The abiotic drivers in the evolution of sexual conflict are a network of interacting, and often opposing, factors. These factors are likely to drive local population-level differences in mating system evolution and variation. Current research stands to benefit from increased attention to tropical regions as well as a purging of long-held biases against tropical biology (Zuk 2016). However, discrete classification of biomes into temperate and tropical categories is likely to be ineffective for future investigations (Machado et al. 2016). These broad classifications retain a prominent level of variation in climate patterns and abiotic environmental factors, possibly making investigations difficult (Machado et al. 2016). This is an area for improvement in current research, which often utilizes or investigates single populations and fails to account for (possibly significant) population-level variation (Machado et al. 2016; Olivero et al. 2017; Fowler-Finn et al. 2019). Interpopulation trait variation could mean that investigation of a singular population is not sufficient to draw conclusions about an entire species and should be considered when studying the abiotic drivers of mating system evolution. Finally, the length of the breeding season may have an appreciable effect on mating system evolution (Burns et al. 2012; Machado et al. 2016; Heldstab 2021), but future investigations will need to decouple the breeding season from other abiotic factors in order to draw accurate conclusions (Connallon 2015; Connallon and Hall 2016; De Lisle et al. 2018; García-Roa et al. 2018; García-Roa et al. 2020).

Acknowledgments

D.W. and M.-K.J. were supported by a National Science Foundation grant (1002566) to the University of Maryland, Baltimore County (UMBC) Louis Stokes Alliance for Minority Participation (LSAMP) program. We are thankful for the expertise of UMBC Librarian Semhar Yohannes, who was instrumental in acquiring resources and reviewing our initial search string. We additionally thank labmates Tyler Brown and Marina Fahim, editor Suzanne Alonzo, and two anonymous reviewers for their critical feedback.

Statement of Authorship

R.B.: methods development/experimental design, data collection, data analysis, data validation, writing—original draft, writing—review and editing; D.W.: data collection, data validation, writing—original draft; M.-K.J.: data collection, data validation, writing—original draft; M.B.: conceptualization, methods development/experimental design, data collection, data analysis, data validation, writing—original draft, writing—review and editing.

Data and Code Availability

Scripts and data files are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.79cnp5hx4; Bacon et al. 2022).

Literature Cited

Adler, M., and R. Bonduriansky. 2014. Sexual conflict, life span, and aging. Cold Spring Harbor Perspectives in Biology 6:a017566. https://doi.org/10.1101/cshperspect.a017566.

Arnqvist, G., and L. Rowe. 2002. Antagonistic coevolution between the sexes in a group of insects. Nature 415:787–789. https://doi.org/10.1038/415787a.

———. 2005. Sexual conflict. Princeton University Press, Princeton, NJ.

Bacon, R., D. Washington, M. K. Johnson, and M. Burns. 2022. Data from: The geography of sexual conflict: a synthetic review. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.79cnp5hx4.

Block, W., G. Baust, F. Franks, I. A. Johnston, and J. Bale. 1990. Cold tolerance of insects and other arthropods. Philosophical Transactions of the Royal Society B 326:613–633. https://doi.org/10.1098/rstb.1990.0035.

Bonduriansky, R. 2014. The ecology of sexual conflict: background mortality can modulate the effects of male manipulation on female fitness. Evolution 68:595–604.

Burns, M., M. Hedin, and J. W. Shultz. 2012. Molecular phylogeny of the leiobunine harvestmen of eastern North America (Opiliones: Sclerosomatidae: Leiobuninae). Molecular Phylogenetics and Evolution 63:291–298. https://doi.org/10.1016/j.ympev.2011.12.025.

———. 2013. Comparative analyses of reproductive structures in harvestmen (Opiliones) reveal multiple transitions from courtship to precopulatory antagonism. PLoS ONE 8:e66767. https://doi.org/10.1371/journal.pone.0066767.

Burns, M., and J. W. Shultz. 2015. Biomechanical diversity of mating structures among harvestmen species is consistent with a spectrum of precopulatory strategies. PLoS ONE 10:e0137181. https://doi.org/10.1371/journal.pone.0137181.

Buzatto, B. A., R. Macías-Ordóñez, and G. Machado. 2013. Macroecology of harvestman mating systems. *In* R. Macedo, ed. Sexual selection: perspectives and models from the Neotropics. Academic Press, London. https://doi.org/10.1016/B978-0-12-416028-6.00005-0.

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. https://doi.org/10.1007/s00265-008-0638-9.

Candolin, U. 1998. Reproduction under predation risk and the trade-off between current and future reproduction in the three-spine stickleback. Proceedings of the Royal Society B 265:1171–1175. https://doi.org/10.1098/rspb.1998.0415.

Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. Trends in Ecology and Evolution 18:41–47. https://doi.org/10.1016/S0169-5347(02)00004-6.

Chown, S., and S. Nicholson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford Scholarship Online. https://doi.org/10.1093/acprof:oso/9780198515494.001.0001.

Clutton-Brock, T. H., and G. A. Parker. 1995. Sexual coercion in animal societies. Animal Behaviour 49:1345–1365. https://doi.org/10.1006/anbe.1995.0166.

Connallon, T. 2015. The geography of sex-specific selection, local adaptation, and sexual dimorphism. Evolution 69:2333–2344. https://doi.org/10.1111/evo.12737.

Connallon, T., and M. D. Hall. 2016. Genetic correlations and sex-specific adaptation in changing environments. Evolution 70:2186–2198. https://doi.org/10.1111/evo.13025.

Corlett, R., and R. B. Primack. 2010. Tropical rain forests: an ecological and biogeographical comparison. 2nd ed. Wiley, Malden, MA. https://doi.org/10.1002/9781444392296.

Côté, I. M., and M. D. Jennions. 2013. The procedure of meta-analysis in a nutshell. Pages 14–24 *in* J. Koricheva, J. Gurevitch, and K. Mengerson, eds. The handbook for meta-analysis in ecology and evolution. Princeton University Press, Princeton, NJ. https://doi.org/10.1515/9781400846184-004.

De Lisle, S., D. Goedert, A. Reedy, and E. Svensson. 2018. Climatic factors and species range position predict sexually antagonistic selection across taxa. Philosophical Transactions of the Royal Society B 373:20170415. https://doi.org/10.1098/rstb.2017.0415.

Dynessius, M., and R. Jansson. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proceedings of the National Academy of Sciences of the USA 97:9115–9120. https://doi.org/10.1073/pnas.97.16.9115.

Eldakar, O. M., D. S. Wilson, M. J. Dlugos, and J. W. Pepper. 2010. The role of multilevel selection in the evolution of sexual conflict in the water strider *Aquarius remigis*. Evolution 64:3183–3189. https://doi.org/10.1111/j.1558-5646.2010.01087.x.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223. https://doi.org/10.1126/science.327542.

Fowler-Finn, K., S. L. Boyer, R. Ikagawa, T. Jeffries, P. C. Kahn, E. M. Larsen, D. Lee, D. Sassen, and M. Smeester. 2019. Qualitative and quantitative comparisons of mating behaviour across multiple populations and six species of leiobunine harvestmen (Arachnida: Opiliones). Behaviour 156:363–390. https://doi.org/10.1163/1568539X-00003545.

Freeman, S., K. Quillin, L. A. Allison, M. Black, E. Taylor, G. Podgorski, and J. Carmichael. 2017. Biological science. 6th ed. Pearson.

García-Roa, R., V. Chirinos, and P. Carazo. 2018. The ecology of sexual conflict: behaviorally plastic responses to temperature variation in the social environment can drastically modulate male harm to females. bioRxiv, https://doi.org/10.1111/1365-2435.13275.

García-Roa, R., F. Garcia-Gonzales, D. W. A. Noble, and P. Carazo. 2020. Temperature as a modulator of sexual selection. Biological Reviews 95:1607–1629. https://doi.org/10.1111/brv.12632.

Heldstab, S. A. 2021. Latitude, life history and sexual size dimorphism correlate with reproductive seasonality in rodents. Mammal Review 51:256–271. https://doi.org/10.1111/mam.12231.

Hollis, B., M. Koppik, K. Wensing, H. Ruhman, and E. Genzoni. 2019. Sexual conflict drives male manipulation of female postmating responses in *Drosophila melanogaster*. Proceedings of the National Academy of Sciences of the USA 117:8437–8444. https://doi.org/10.1073/pnas.1821386116.

Kaneshiro, K. 2009. Sexual Selection. Pages 917–921 *in* V. Resh, ed. Encyclopedia of insects. 2nd ed. Academic Press, London. https://doi.org/10.1016/B978-0-12-374144-8.00243-5.

Kasumovic, M. M., M. J. Bruce, M. C. B. Andrade, and M. E. Herberstein. 2008. Spatial and temporal demographic variation drives within-season fluctuations in sexual selection. Evolution 62:2316–2325. https://doi.org/10.1111/j.1558-5646.2008.00446.x.

Machado, G., B. Buzatto, S. García-Hernández, and R. Macías-Ordóñez. 2016. Macroecology of sexual selection: a predictive conceptual framework for large-scale variation in reproductive traits. American Naturalist 188:S8–S27. https://doi.org/10.1086/687575.

Michalczyk, Ł., A. L. Millard, O. Y. Martin, A. J. Lumley, B. C. Emerson, and M. J. G. Gage. 2011. Experimental evolution exposes female and male responses to sexual selection and conflict in *Tribolium castaneum*. Evolution 65:713–724. https://doi.org/10.1111/j.1558-5646.2010.01174.x.

Monteiro, N. M., and D. O. Lyons. 2012. Stronger sexual selection in warmer waters: the case of a sex role reversed pipefish. PLoS ONE 7:e44251. https://doi.org/10.1371/journal.pone.0044251.

Mora, C., D. P. Tittensor, S. Adl, A. G. B. Simpson, and B. Worm. 2011. How many species are there on earth and in the ocean? PLoS Biology 9:e1001127. https://doi.org/10.1371/journal.pbio.1001127.

Olivero, P., C. Mattoni, and A. Peretti. 2017. Differences in mating behavior between two allopatric populations of a Neotropical scorpion. Zoology 123:71–78. https://doi.org/10.1016/j.zool.2017.06.009.

Parker, G. A. 1979. Sexual selection and sexual conflict. Pages 123–166 *in* M. S. Blum and N. A. Blum, eds. Sexual selection and reproductive competition in insects. Academic Press, London. https://doi.org/10.1016/B978-0-12-108750-0.X5001-0.

———. 2006. Sexual conflict over mating and fertilization: an overview. Philosophical Transactions of the Royal Society B 361:235–259. https://doi.org/10.1098/rstb.2005.1785.

Perry, J., and L. Rowe. 2018. Sexual conflict in its ecological setting. Philosophical Transactions of the Royal Society B 373:20170418. https://doi.org/10.1098/rstb.2017.0418.

Pizzari, T., and R. Snook. 2003. Sexual conflict and sexual selection: chasing away paradigm shifts. International Journal of

Organic Evolution 57:1223–1236. https://doi.org/10.1111/j.0014-3820.2003.tb00331.x.

———. 2007. Sexual conflict and sexual selection: measuring antagonistic coevolution. Evolution 58:1389–1393. https://doi.org/10.1111/j.0014-3820.2004.tb01717.x.

Plesnar-Bielak, A., and A. Łukasiewicz. 2021. Sexual conflict in a changing environment. Cambridge Philosophical Society 96:1854–1867. https://doi.org/10.1111/brv.12728.

Plesnar-Bielak, A., A. M. Skwierzyńska, and J. Radwan. 2020. Sexual and ecological selection on a sexual conflict gene. Journal of Evolutionary Biology 33:1433–1439. https://doi.org/10.1111/jeb.13680.

Rice, W. R. 2000. Dangerous liaisons. Proceedings of the National Academy of Sciences of the USA 97:12953–12955. https://doi.org/10.1073/pnas.97.24.12953.

Schärer, L., L. Rowe, and G. A. Arnqvist. 2012. Anisogamy, chance and the evolution of sex roles. Trends in Ecology and Evolution 27:260–264. https://doi.org/10.1016/j.tree.2011.12.006.

Schenkel, M. A., I. Pen, L. W. Beukeboom, and J. C. Billeter. 2018. Making sense of intralocus and interlocus sexual conflict. Ecology and Evolution 8:13035–13050. https://doi.org/10.1002/ece3.4629.

Titley, M. A., J. L. Snaddon, and E. C. Turner. 2017. Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. PLoS ONE 12:e0189577. https://doi.org/10.1371/journal.pone.0189577.

Wensing, K. U., M. Koppik, and C. Fricke. 2017. Precopulatory but not postcopulatory male reproductive traits diverge in response to mating system evolution in *Drosophila melanogaster*. Ecology and Evolution 7:10361–10378. https://doi.org/10.1002/ece3.3542.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, NJ.

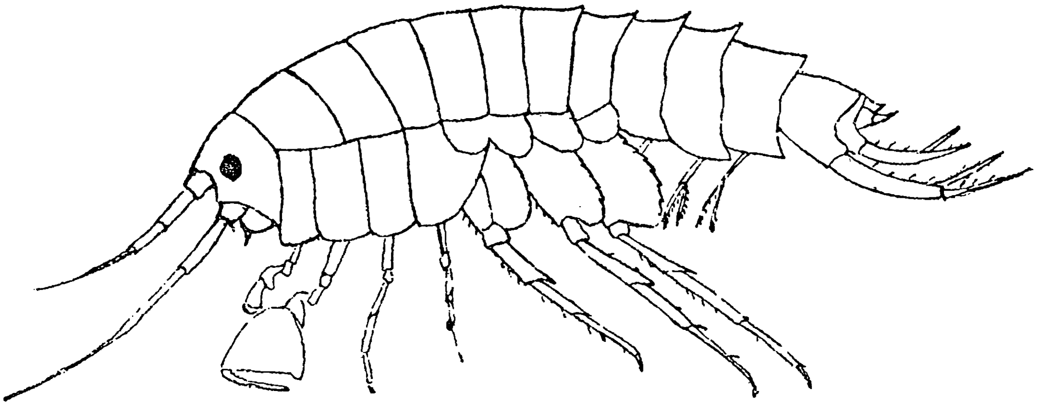
Yun, L., P. J. Chen, K. E. Kwok, C. S. Angell, H. D. Rundle, and A. F. Agrawal. 2018. Competition for mates and the improvement of nonsexual fitness. Proceedings of the National Academy of Sciences of the USA 115:6262–6767. https://doi.org/10.1073/pnas.1805435115.

Yun, L., P. Chen, A. Singh, A. Agrawal, and H. Rundle. 2017. The physical environment mediates male harm and its effect on selection in females. Proceedings of the Royal Society B 284:20170424. https://doi.org/10.1098/rspb.2017.0424.

Zerbe, P., M. Clauss, D. Codron, L. B. Lackey, E. Rensch, J. W. Streich, J. M. Hatt, and D. W. H. Muller. 2012. Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. Biological Reviews 87:965–990. https://doi.org/10.1111/j.1469-185X.2012.00238.x.

Zuk, M. 2016. Temperate assumptions: how where we work influences how we think. American Naturalist 188:S1–S7. https://doi.org/10.1086/687546.

Symposium Editor: Suzanne H. Alonzo



“Some [new species] are also noteworthy as comparatively deep-water forms of a family commonly regarded preëminently littoral. I believe no *Orchestidæ* have heretofore been found at a depth so great as sixty-six fathoms.” Figured: “*Allorchestes latimanus*.” Quoting W. Faxon in the review of “The Crustacea of Lake Titicaca” (*The American Naturalist*, 1871, 4:754–763).