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Competition and climate affect body size and sexual size dimorphism in pine sawyer beetles

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Abstract

The importance of interspecific competition in structuring communities of plant-eating insects has been somewhat controversial. If interspecific competition is ever important for phytophagous insects, it is likely to be observed in the insect guild that feeds in the phloem of trees. We tested for signals of interspecific competition in co-occurring species of pine sawyer beetles *Monochamus* Megerle (Coleoptera Cerambycidae), generally the largest phloemophagous insects in pines. We evaluated patterns of body size and its correlation with other life-history traits. By studying pine sawyer beetles in different areas (Northeast USA, Southeast USA and Portugal) we assessed the interaction with climate. As predicted under the hypothesis of interspecific competition, there were always clear size differences among coexisting species. As predicted if competition is asymmetric, smaller species were less abundant and emerged earlier than the larger species. In the larger and numerically dominant species, sexual size dimorphism was more pronounced and the sex ratio was skewed towards females. In the smaller species, males emerged earlier (protandry), whereas the larger species lacked differences in emergence time or displayed protogyny. Effects of climate only seem to have been expressed in the larger dominant species of each area, whereas the effects of competition in smaller species probably overshadow the effects of climate.

Key words: egg size, fecundity, *Monochamus*, protandry, protogyny, Rensch's rule.

Introduction

In phytophagous insects, the acceptance of interspecific competition as a driving force in structuring communities has been controversial (Lawton and Strong, 1981; Kaplan and Denno, 2007). A review by Denno *et al.* (1995) did found that interspecific competition can be important among mandibulate herbivores feeding in concealed niches, and especially when they are closely related, introduced, sessile, and aggregative. Furthermore, the competitive interactions among co-occurring phytophagous insects tend to be highly asymmetrical (Kaplan and Denno, 2007). An important determinant of asymmetries in competitive interactions is a difference in body size, which has a strong impact on life history strategies and population dynamics (Bassar *et al.*, 2016). Body-size asymmetries result in size-dependent trophic interactions, with potential to organize the structure and function of communities. They can be central to resource-partitioning and niche segregation, allowing species coexistence (Werner and Gilliam, 1984). Among aggregated insect herbivores that feed in concealed niches, intraguild predation is especially important (Coulson *et al.*, 1980; Schoeller *et al.*, 2012; Jones *et al.*, 2015). This is a special case of species interaction that combines competition and predation ("killing and eating among potential competitors"; Polis *et al.*, 1989), and its direction and strength between competitors are very dependent on differences in size (Wissinger, 1992; Arim and Marquet, 2004). Nonetheless, the role of differences in body size on competitive interactions in insects has not received much attention (but see Messina and Peterson, 2004).

Within species, sexual size dimorphism (SSD) is a discontinuous variation in body size between sexes (Teder and Tammaru, 2005; Stillwell *et al.*, 2010). SSD often results from selective pressures related to sexual selection, with fecundity selection on females and sexual selection on males being the major general sources of selection favouring larger size in each gender (Fairbairn, 1997; Stillwell *et al.*, 2010). Larger insect females generally produce more or larger offspring (Honek, 1993). Larger insect males can have increased mating success due to advantages in acquiring territory, providing nuptial gifts, and in male-male competition (Hughes and Hughes, 1982; Fox *et al.*, 2006; Serrano-Meneses *et al.*, 2007). However, increased SSD can also be favoured under natural selection because it facilitates resource partitioning between the sexes, decreasing the negative effects of intraspecies competition, determining the species niche (Fairbairn, 1997; Pincheira-Donoso *et al.*, 2018). Analysis of patterns in SSD among taxa and environments can provide insights into the sources of selection that favour large versus small size (Stillwell *et al.*, 2010). Furthermore the allometry between female body size and egg size can also lead to asymmetric competition among immature stages. Hatchling size, which is related with egg size, can create initial asymmetries that will determine the strength and directions of coexistent species interactions throughout development (Parker and Begon, 1986; Wissinger, 1992).

Climate, mostly through the effect of temperature, is generally known to have a strong effect not only on body size, but also at other levels of organization such as egg size. In some insects species there are clear patterns of geographic variation in body size related to temperature, that are interpretable in terms of life history theory (Ayres and Scriber, 1994; Parry *et al.*, 2001; Blanckenhorn *et al.*, 2006; Stillwell *et al.*, 2007; Pimentel *et al.*, 2010; 2012). However, the existence of biogeographical clines in insect body size is not universally expressed and straightforward

(Shelomi, 2012). Rapid environmental change in many ecosystems has increased the relevance of understanding how climate affects the relationship between fitness and body size (Horne *et al*., 2017; Baar *et al*., 2018).

The genus *Monochamus* Megerle (Coleoptera Cerambycidae), the pine sawyer beetles, can be found throughout pine forests of the northern hemisphere, subsisting in a wide range of climates, from boreal to subtropical. They are medium to large size wood borers and are associated by phylogeny and ecology with other members of the Cerambycidae and Buprestidae families. Adults feed on twigs of healthy pines and then oviposit into the bark of dying or recently dead pines. Larvae feed on fresh phloem, and late larvae bore a U-shaped gallery into the xylem where they pupate (Linsley and Chemsak, 1984; Akbulut and Stamps, 2012). These insects are considered secondary pests, affecting weakened or already dying pine trees, but can decrease the value of timber. They have been the focus of research mostly due to being the vector of the pinewood nematode *Bursaphelenchus xylophilus* Steiner et Buhrer (Nematoda Aphelenchoididae), the causal agent of the pine wilt disease (Akbulut and Stamps, 2012; Pimentel *et al*., 2014; Firmino *et al*., 2017).

Monochamus are generally the larger species of the pine phloem feeding guild, which includes several smaller bark beetles species and other larger wood borers. Within this guild, asymmetric competitive interactions favour larger and more mobile cerambycid larvae and intraguild predation is common (Coulson *et al*., 1980; Schoeller *et al*., 2012). In general, bark and wood-boring insects provide a likely arena for important interspecific competition among closely related beetle species who all feed upon a shared limiting resource (Jones *et al*., 2015).

Multiple species of *Monochamus* often co-occur within the same forests and the same host trees, with known competitive interactions where size differences can be crucial (Linsley and Chemsak, 1984; Hughes and Hughes, 1987; Koutroumpa *et al*., 2013; Pimentel *et al*., 2014). All these attributes make the pine sawyer beetles potentially good models to assess signals of interspecific competition, and its role on shaping the ecological niche of close related plant feeding insects. Furthermore, their wide distribution, also allows an assessment of interactions between competition and climate. Thus, in the present work we measured several life-history traits potentially implicated in competitive interactions and niche differentiation (phenology, adult size, including SSD and egg size), in sympatric and syntopic species of pine sawyer beetles subsisting under distinct climates. We expect to contribute to a better understanding on how competitive interactions modulates phytophagous insect species life history traits and coexistence.

Materials and methods

Collection of field specimens

Specimens of *Monochamus* species were obtained from two autochthonous pine forests in the eastern USA (VT and LA), and one in Portugal (PT). The two forests in the USA were separated by about 2500 km, contained different species of pine, and had different climates: 1) a forested region in the northeast (Vermont and New Hampshire) with mainly white pine *Pinus strobus* L. and some red pine *Pinus resinosa* Aiton (VT: 43°42'N 072°17'W, 162 m asl); and 2) the Kisatchie National Forest, in Central Louisiana (LA - 31°20'N 92°24'W, 36 m asl), with longleaf pine *Pinus palustris* Miller, loblolly pine *Pinus taeda* L., slash pine *Pinus elliottii* Engelm., and shortleaf pine *Pinus echinata* Miller. Our study forest in Portugal was a coastal region in the southwest (PT: 38°08'N 8°43'W, 39 m asl) that is chiefly *Pinus pinaster* Aiton stands, occasionally interspersed with *Pinus pinea* L., *Eucalyptus globulus* Labillardiere and *Quercus suber* L. VT has a humid continental climate (Köppen), with long, cold, snowy winters, and warm humid summers, an annual average temperature of 9.5 °C, and average temperatures of the hottest summer months between 19.5-22.5 °C. Precipitation is well-spread throughout the year with an annual average of 1,132 mm. LA has a humid subtropical climate (Köppen), with hot and humid summers and mild winters, an annual average temperature of 19.4 °C, and average temperatures of the hottest months between 27-28.5 °C. The area receives abundant rainfall year-round with an average of 1,533 mm. In PT the climate is Mediterranean with mild winters and hot dry summers; average annual temperature is 16.0 °C and annual precipitation is 507 mm. There is a characteristic summer dry season (typically from June to August), when average temperature increases to 19.5 °C and precipitation drops to about 5 mm per month (NowData - NOAA Online Weather Data, National Oceanic and Atmospheric Administration, retrieved 2016-07-16.).

Monochamus spp. adults are generally attracted to host volatiles and bark beetles' pheromones, which indicates a suitable host - a damaged or freshly dead pine tree. In fact, blends of these compounds associated with multiple-funnel traps were found to be highly effective for monitoring pine sawyers beetles, with consistency of results across large geographic areas suggesting similar selection pressures on different species of the genus across different climates (Miller *et al*., 2013). Thus, in the present work we trapped live pine sawyers beetles in the wild using Lindgren Multi-Funnel Traps® with 12 black funnels, adapted for an efficient trapping of large insects, baited with α-pinene (170 g, releasing ~2 g/day) and Ipsenol (100 mg, releasing ~500 µg/d) (Synergy Semiochemicals Corp.). This occurred during the spring/summer 2011 in the USA, and 2012 in PT. In each forest, we deployed five traps separated from each other at least 3 km (further details in Pimentel *et al*., 2014 and Firmino *et al*., 2017). As much as possible, the traps were placed in areas with recently dead trees. The traps were deployed sufficiently early in the season that there were always at least 2 weeks before we captured the first *Monochamus* and were then checked weekly until at least 2 weeks after new captures ceased. We expected with this methodology to obtain a representative sample of mature adults throughout the flight season in each area.

All captured *Monochamus* were identified and sexed, and the body length of each beetle was measured with a digital caliper (range 0-150 mm, resolution 0.01). The female abdomen was opened and all the eggs in the ovaries counted - an indication of fecundity. *Monochamus* eggs have the shape of a prolate ellipsoid, and in each female, the longest axis of three randomly selected eggs was measured with a digital caliper (range 0-150 mm, resolution 0.01). The average of these three measurements was considered the egg size of that particular female.

Statistical analysis

We tested for differences among *Monochamus* species in body size, egg number and size with analysis of variance (one way ANOVA), followed by Tukey's honestly significant difference test (Tukey HSD). We tested for differences in emergence time (Julian date) between species, and for differences in traits between sexes with two sample *t*-tests. Interspecific variation in the different traits was assessed through Pearson Correlation. We tested for patterns in the number and size of eggs with a general linear model that included species and origin of *Monochamus* (5 classes), body size of the female adult (continuous variable), and species × body size (to test for heterogeneity among species in the relationships with body size). Regression analyses were performed using the software OriginPro© 8 SR0 (1991-2007 OriginLab Corporation).

Results

In both of forests studied in the USA, we found pairs of *Monochamus* species: in VT the white-spotted sawyer *Monochamus scutellatus* (Say) and the northeastern pine sawyer *Monochamus notatus* (Drury); in LA the Carolina sawyer *Monochamus carolinensis* (Olivier) and the southern pine sawyer *Monochamus titillator* (F.). In Portugal only the black pine sawyer *Monochamus galloprovincialis* (Olivier) was found. By far, the largest number of *Monochamus* captures were in LA, during a long flight season of seven months. Here, there was a clear difference in the flight phenology of the two species collected: *M. carolinensis* averaged 24.7 days earlier than for *M. titillator* (two sample t-test: t = 9.85, df = 1904, $P < 0.001$). *Monochamus* were much less abundant in the other two study regions. In PT only a few dozen adults of *M. galloprovincialis* were trapped, also over a long flight season of seven months. In VT, during a much shorter flight season of just three months, few adults of two species were trapped, also with significant differences in emergence time between them: *M. scutellatus* capture dates averaged 38.6 days before *M. notatus* (t = 5.99, df = 44, $P < 0.001$, table 1).

Table 1. Portion of the year in which pine sawyer beetles (*Monochamus*) were trapped (flight season), and number of adults from each species captured in northeast USA (VT), southeast USA (LA), and Portugal (PT); sex ratio of each species, and average difference in number of days of emergence of males in relation to females.

Area	Flight season	*Monochamus* species	Number	sex ratio ♀/♂	Number of days ♂ preceded ♀	
VT	July-September	*M. scutellatus*	19	0.58	-21.7**	Protandry
		M. notatus	27	2.0	5.5	No differences
LA	April-October	*M. carolinensis*	615	1.11	-12.2**	Protandry
		M. titillator	1290	1.48	2.1	No differences
PT	April-October	*M. galloprovincialis*	81	1.13	28.1*	Protogyny

Average difference in days of days of emergence tested with *t*-test statistic: **significant at $P < 0.01$; *significant at $P < 0.05$

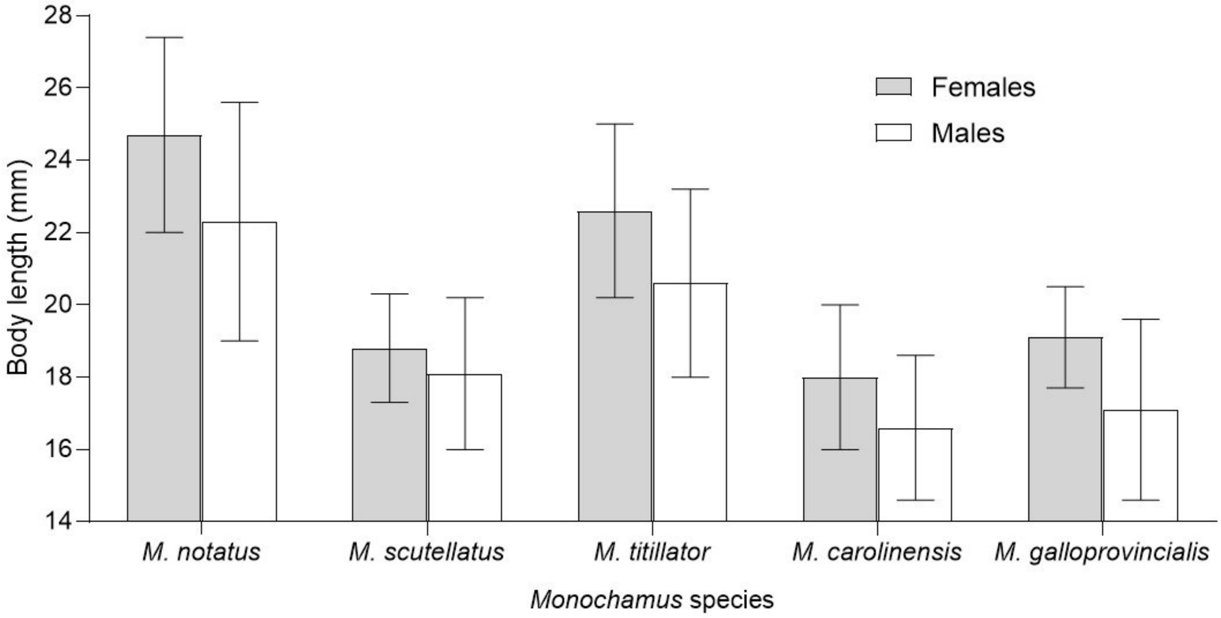

Figure 1. Mean ± SD body length in the different *Monochamus* species.

The body length of female adults varied by up to 36% among species, with *M. notatus* being the largest species followed by *M. titillator* (one-way ANOVA $F_{4,770}$ = 163.2, $P < 0.001$; Tukey HSD *M. notatus* > *M. titillator* > *M. galloprovincialis* ≈ *M. scutellatus* ≈ *M. carolinensis* $P < 0.01$; figure 1). The body length of males also varied among species, but in this case the two larger species -*M. notatus* and *M. titillator*- had similar size males (one-way ANOVA $F_{4,811}$ = 132.1, $P < 0.001$; Tukey HSD *M. notatus* ≈ *M. titillator* > *M. galloprovincialis* ≈ *M. scutellatus* ≈ *M. carolinensis* P<0.01; figure 1). There were more eggs in abdomens of female *M. titillator* (Mean ± SD 23.6 ± 6.9) than in the other four species, which were similar (16.0 ± 6.1 to 19.9 ± 5.3) (one-way ANOVA $F_{4,770}$ = 44.9, P <0.001; Tukey HSD *M. titillator* > *M. notatus* ≈ *M. galloprovincialis* ≈ *M. scutellatus* ≈ *M. carolinensis* $P < 0.05$). Egg size was broadly correlated with female body size across species. *M. notatus*, the largest species, produced the largest eggs (Mean ± SD 4.55 ± 0.23 mm), followed by the second largest species, *M. titillator*, (4.05±0.27 mm). The three smaller species produced similarly smaller eggs (3.37 ± 0.22 to 3.47 ± 0.25 mm) (one-way ANOVA $F_{4,770}$ = 237.1, $P < 0.001$; Tukey HSD *M. notatus* > *M. titillator* > *M. galloprovincialis* ≈ *M. scutellatus* ≈ *M. carolinensis* $P < 0.01$).

Average male size was always smaller than average female size (figure 1), and significantly so in all species except *M. scutellatus* (two sample *t* test $P < 0.05$ for all significant differences). The correlation between female body size and size differences between the sexes was positive but not significant (Pearson correlation R = 0.42, P = 0.47, n = 5 species). Sex ratio tended to favour females, but with variation among species and not in the case of *M. scutellatus* (table 1). There was a positive correlation between average female body size and ♀/♂ sex ratio (R = 0.88, P = 0.051). The relative timing of emergence of the two genders also differed among species, with two species presenting protandry, one protogyny, and no differences in the other two species (table 1).

Monochamus species were similar in that (1) an average sized female carried about 20 eggs, (2) eggs were typically 3 to 5 mm in length and (3) females with larger bodies carried relatively more eggs that tended to be a bit larger. However, the details varied among species (figure 2). The average number of eggs per female varied by about 30% among species (least square mean ± SE = 16.0 ± 1.0, 17.0 ± 0.4, 18.8 ± 0.8, 19.9 ± 2.0, and 23.6 ± 0.3 eggs for *M. galloprovincialis*, *M. carolinensis*, *M. notatus*, *M. scutellatus*, and *M. titillator*, respectively; $F_{4,\ 765}$ = 3.91, P = 0.004). Overall, larger females tended to carry more eggs ($F_{1,\ 765}$ = 16.14, $P < 0.0001$), but the relationship between egg number and body size varied among species. From small to large body size (10th to 90th percentile), the number of eggs increased by about 6 in *M. notatus* to about 12 in *M. titillator* (fecundity increases of 30% in *M. notatus* and 51-56% in *M. carolinensis*, *M. galloprovincialis*, and *M. titillator*; figure 2). This heterogeneity among species in the slope of egg number vs. body size was significant (Species × Body size: $F_{4,\ 765}$ = 3.43, P = 0.009). The average size of eggs varied by about 25% among species (mean ± SE = 3.47 + 0.04, 3.39 + 0.02, 4.55 + 0.05, 3.37 + 0.08, and 4.05 + 0.01 mm for *M. galloprovincialis*, *M. carolinensis*, *M. notatus*, *M. scutellatus*, and *M. titillator,* respectively; $F_{4,\ 765}$ = 36.67, $P < 0.0001$). Egg size tended to increase with body size ($F_{1,\ 765}$ = 11.91, $P < 0.001$, but less strongly than for egg number; from small to large body size (10th to 90th percentile), the typical increase in egg size was only 7-12%.

Discussion

Body size and competitive interactions

In two of our three study areas, we found pairs of co-occurring species of *Monochamus*, and in both cases one species was considerably smaller and had its flight season earlier in the year: *M. scutellatus* vs *M. notatus* in Northeast North America and *M. carolinensis* vs *M. titillator* in Southeast North America. Both these pairs of species were found in previous works to directly compete for fresh phloem from recently dead trees during larval development (Coulson *et al.*, 1980; Hughes and Hughes, 1987; Schoeller *et al.*, 2012). Fresh pine phloem is an ephemeral and limiting resource, thus the likelihood of species coexistence is enhanced by any features of their biology that lessen competition. We propose that differences in body size play an important role in this community for resource partitioning and coexistence. Life-history theory predicts that body size is positively correlated with development time (Roff, 1992), which is broadly evident for insects (García-Barros, 2000). Thus, if two sympatric *Monochamus* species start larval development at the same time, all other things being equal, individuals of the smaller species will tend to emerge earlier. If there are early differences in larval body size, this will lead to increasingly asymmetric competition, perhaps favouring earlier cessation of larval feeding (and therefore smaller adult size) in one species, which would facilitate their coexistence.

In fact, we found that interspecific variation in egg size follows closely the interspecific variation in female body size. On the other hand, although females of *M. titillator* tended to have more eggs in their abdomens (an indication of fecundity), this parameter was surprisingly similar in the other *Monochamus* species, and we did not found a clear interspecific relation between body size and potential fecundity, contrary to the general relationship in insect species (Honek, 1993). It was proposed that the evolution of adult size in insects is partially determined by an allometric link between adult size and egg size, and thus with hatchlings size and length of larval development (Roff, 1992; García-Barros, 2000). Thus, it seems that egg size in *Monochamus* species is under strong selection, probably determining initial size asymmetries within the guild, as well the length of development and final size, limiting an increase in fecundity in larger species. However, within species, an increase in female body size has a larger effect on the number of eggs in the ovaries (30-56% increase), than on their size (7-12%). This is commonly observed in insects (García-Barros, 2000), and has been attributed to a stronger relationship between egg number and maternal fitness than between egg size and maternal fitness, thus following the theoretical pre-

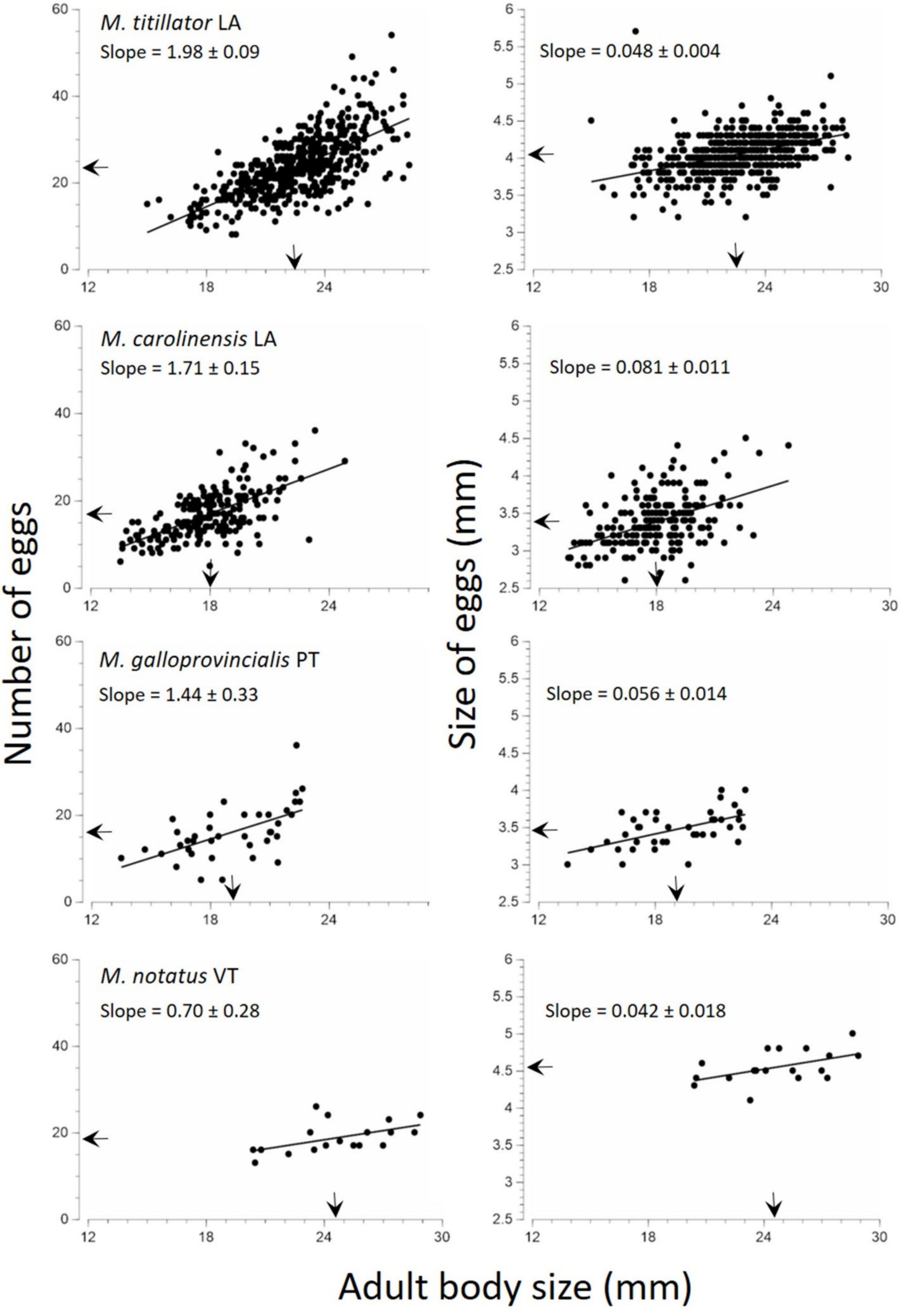

Figure 2. Number of eggs (left) and size of eggs (right) vs body size for four populations of *Monochamus*. (*M. scutellatus* not shown here due to small sample size: N = 7). Insets indicate slopes. Arrows indicate means.

diction that egg number should increase more rapidly than egg size for a given increase in female size (Parker and Begon, 1986; Hendry *et al*., 2001). Thus, within *Monochamus* species gains in female body size will result in higher fecundity, while maintaining an optimum egg size that is species specific.

The larger *Monochamus* species was more abundant than the smaller species in both regions where two species co-occur (table 1), which is consistent with there being a competitive advantage to being larger.

Gender effects

Competitive interactions in sympatric *Monochamus* species also seem to impact sexual size dimorphism (SSD) and sex ratio. *Monochamus* females are larger than males, as in most insect species (Stillwell *et al*., 2010). In *Monochamus* species that did not have a larger co-occurring congener (*M. galloprovincialis*, *M. titillator* and *M. notatus*), females were more abundant than males and SSD was more pronounced compared to species competing with a larger congener (*M. scutellatus* and *M. carolinensis*). Our findings are in agreement with the most common pattern found in insects, in which species with female-biased SSD show an increase in SSD with increasing body size, contrary to the general Rensch's rule, that states the opposite. The explanation for observed patterns in insects is that female size is more sensitive to environmental conditions than male size; under good conditions, there is a larger relative increase in female than male size (Teder and Tammaru, 2005). If female *Monochamus* are under a stronger evolutionary pressure to become larger than males, and considering that becoming larger implies a longer development time (Teder, 2014), then females of smaller species will be more affected by asymmetric competition than males. This possibly will result in higher mortality in females of the smaller species, and/or pupation at a smaller size, explaining the observed patterns. Furthermore, *Monochamus* larvae are facultative intraguild predators, and larger species benefit from the extra nutrients obtained by consuming larvae of smaller species (Coulson *et al*., 1980; Schoeller *et al*., 2012), which would likely benefit females more than males.

We found interspecific variation in the relative timing of adult activity by males and females: *M. galloprovincialis* displayed protogyny - females emerging before males - whereas *M. scutellatus* and *M. carolinensis* displayed protandry - males emerging before females - and *M. titillator* and *M. notatus* displayed no gender difference in adult phenology (table 1). Protandry is common in insects (Bulmer, 1983) and may be a byproduct of selection for female-biased SSD (Morbey, 2013; Teder, 2014), due to the relationship between body size and length of development. However proximate genetic mechanisms determining adult insect emergence can be important, and these are under stronger selection in males than in females (Gu *et al*., 2014). Protandry is in fact considered advantageous because it maximizes mating opportunities for males while minimizing the pre-reproductive period for females, particularly in short lived insects, and those in which females mate only once, shortly after emergence (Fagerström and Wiklund, 1982; Bulmer, 1983; Zonneveld and Metz, 1991). Increased sexual selection due to intense competition among individuals of the chosen sex, generally males, can result in protandry (Bulmer, 1983; Møller, 2004). However protogyny occurs far too often among insects to exclude an evolutionary explanation (Honek, 1997). Theoretical models point to protogyny being a better strategy when female survival is higher than male survival, especially in scenarios where females are long-lived, as long-lived females do not risk much in terms mating failure (Degen *et al*., 2015). In the case of *Monochamus* spp., if emergence time was simply a byproduct of SSD and development length, protandry should be the norm within the genus, especially so in larger species with more pronounced SSD. However it was only observed in smaller species with lower SSD. *Monochamus* adults live for approximately two months under laboratory conditions (Pershing and Linit, 1986), requiring at least 10-15 days to reach sexual maturation (Koutroumpa *et al*., 2008). The relatively long life span of pine sawyer's adults, and the fact that females take some time to reach sexual maturity after emergence, does not give much advantage to males emerging early in the season, explaining the occurrence of protogyny, or no difference in emergence time between the genders. Adult sex ratio is a key factor affecting sexual competition, with male-to-male competition increasing with male biased sex ratio (Weir *et al*., 2011). In the case of *Monochamus*, protandry was observed in the two species with the most male biased sex ratio, where the females most likely suffer higher mortality due to asymmetrical competition. Thus protandry may have evolved within the genus due to increased sexual competition among males coupled with lower survival of females.

Climate effects

In all three study areas - Northeast North America, Southeast North America, and Portugal - the largest insect feeding on pine phloem is a *Monochamus* species. However the size of the largest phloeophagous insect varied among these regions. *M. notatus* from the northern USA was the largest species, followed by *M. titillator* from the wet subtropical USA. The smallest was *M. galloprovincialis* from a Mediterranean climate in Portugal, which were of similar size to the smallest *Monochamus* spp. in our two other study regions.

Temperature, aridity, and length of the dry season have all been reported to affect insect body size either negatively or positively (Le Lagadec *et al*., 1998; García-Barros, 2000; Davidowitz, 2008). In arid environments, larger insects might experience reduced risk of desiccation (Le Lagadec *et al*., 1998). On the other hand, smaller insects could be favoured in arid environments because they need less food, which tends to be more limiting when precipitation is low (Davidowitz, 2008). In fact, our smallest numerically dominant wood borer (*M. galloprovincialis*) was found in our most arid study region, and the greatest numerical advantage of large vs. smaller species was in our wettest climate (*M. titillator* captures in LA were twice that of *M. carolinensis*). Our results match the model of Davidowitz (2008) which predicts that fitness as function of body size tends to shift toward favouring large body size under climates that favour higher productivity of basal resources.

M. notatus was the largest pine sawyer recorded in our study, inhabiting the coldest climate, at the highest latitude, being its females about 10% larger than females of *M. titillator*. The relationship between insect body size and environmental temperature is complex and finding general patters have proved to be elusive. On one hand, low ambient temperature can result in smaller adult size due to shorter growing seasons, implying less time and resources for individuals to mature, and also a need for longer time to attain a larger body size since growth rates are dependent on environmental temperature - the so called converse Bergmann's clines (Roff, 1992; Blanckenhorn and Demont, 2004). However, in the present case it does not seem that low environmental temperatures limit the size of the dominant pine sawyers in the guild, contrary to what happens with precipitation. We studied a limited number of species, but an hypothesis to explain our findings is that *Monochamus* life cycle does not seem to be dependent on specific host phenology, which can be related with the length of the development season in insects (Ayres and Scriber, 1994), since females oviposit in recently dead pines, which can occur throughout the flight season. There is also evidence that *Monochamus* life cycle can evolve to be univoltine or bivoltine (Pimentel *et al*., 2014; Firmino *et al*., 2017), or even require two years to be completed depending on climate (Tomminen, 1993). Thus, adaptation of voltinism to local environmental temperature, and independence from host phenology, possibly makes *Monochamus* not so restricted by season length.

The foremost hypotheses to explain larger sizes in colder environments (Bergmann's rule) are the heat conservation hypothesis and the starvation resistance hypothesis (Blackburn *et al*., 1999; Scriven *et al*., 2016). Temperature effects on growth rate and final size were also considered as potential explanation: higher environmental temperatures lead to faster development rates, shorter development times, and lower final mass, and such observations were formalized in the temperature-size rule (Atkinson, 1994). Not much is known about *Monochamus* physiology, or the potential advantage of growing bigger in colder climates, but if there is an advantage, it is only expressed in the larger dominant species. No difference was found in body size between the two smaller species -*M. scutellatus* and *M. carolinensis*- likely to suffer from asymmetric competition from the dominant pine sawyers. On these species, the effects of competition probably overshadow any possible ecogeographical effect on life-history traits.

A relationship between size and ambient temperature has also been found at other levels of organization besides whole body mass. Particularly, egg size tends to increase with decreasing environmental temperature, independent of the effect of maternal size (Atkinson *et al*., 2001). Larger eggs can be adaptive in colder environments due to a faster post-embryonic development rate as a result of increased hatchling mass, which is advantageous when the season length decreases (Ayres and Schriber, 1994; Gillooly *et al*., 2002). Larger egg size also confers greater tolerance to temperature variation, leading to higher hatchability under harsh climatic conditions (Fischer and Fiedler, 2001). We did found that *M. notatus* females produce the larger eggs, but this maybe due to the allometric relation between egg size and adult size. The larger females of *M. notatus* also stand out in that they are less efficient in translating an increase in body length into an increase in fecundity than any of the other *Monochamus* species, ending up with a lower number of eggs in their ovaries than *M. titillator*. No such difference was found in relation to intraspecific variation in egg size, as indicated by the slopes of regressions between female body size and reproductive output (figure 2). Since ectotherm physiology is strongly temperature-dependent, insect fecundity might be limited by temperature, and the potential fecundity advantage of a large size may not be fully realized in colder environments (Berger *et al*., 2008).

Conclusions

In the present work we found evidence that body size plays a crucial role in a specific guild of phytophagous insects, leading to asymmetric competitive interactions among species. Interactions between competition and body size are determinant in several life-history traits, such as SSD, sex ratio and relative timing of emergence in adults of both genders (protogyny vs protandry). Asymmetric competition also seems to affect the expression of ecogeographical rules, which are more evident in large and dominant species, while in smaller species the effects of competition probably overshadow any possible ecogeographical effect on life-history traits.

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References

AKBULUT S., STAMPS W. T., 2012.- Insect vectors of the pinewood nematode: a review of the biology and ecology of *Monochamus* species.- *Forest Pathology*, 42: 89-99.

ARIM M., MARQUET P. A., 2004.- Intraguild predation: a widespread interaction related to species biology.- *Ecology Letters*, 7: 557-564.

ATKINSON D., 1994.- Temperature and organism size - a biological law for ectotherms?- *Advances in Ecological Research*, 25: 1-58.

Atkinson D., Morley S. A., Weetman D., Hughes R. N., 2001.- Offspring size responses to maternal temperature in ectotherms, pp. 269-285. *In environment and animal development: genes, life histories and plasticity* (Atkinson D., Thorndyke M. Eds).- BIOS Scientific Publishers, Oxford, UK.

Ayres M. P., Scriber J. M., 1994.- Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae).- *Ecological Monographs*, 64: 465-482.

Baar Y., Friedman A. L. L., Meiri S., Scharf I., 2018.- Little effect of climate change on body size of herbivorous beetles.- *Insect Science*, 25: 309-316.

Bassar R. D., Childs D. Z., Rees M., Tuljapurkar S., Reznick D. N., Coulson T., 2016.- The effects of asymmetric competition on the life history of Trinidadian guppies.- *Ecology Letters*, 19: 268-278.

Berger D., Walters R., Gotthard K., 2008.- What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly.- *Functional Ecology*, 22: 523-529.

Blackburn T. M., Gaston K. J., Loder N., 1999.- Geographic gradients in body size: a clarification of Bergmann's rule.- *Diversity and Distributions*, 5: 165-174.

Blanckenhorn W. U., Demont M., 2004.- Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum?- *Integrative and Comparative Biology*, 44: 413-424.

Blanckenhorn W. U., Stillwell R. C., Young K. A., Fox C. W., Ashton K. G., 2006.- When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude?- *Evolution*, 60: 2004-2011.

Bulmer M., 1983.- Models for the evolution of protandry in insects.- *Theoretical Population Biology*, 23: 314-322.

Coulson R. N., Pope D. N., Gagne J. A., Fargo W. S., Pulley P. E., Edson L. J., Wagner T. L., 1980.- Impact of foraging by *Monochamus titillator* (Col.: Cerambycidae) on within-tree populations of *Dendroctonus frontalis* (Col.: Scolytidae).- *Entomophaga*, 25: 155-170.

Davidowitz G., 2008.- Population and environmental effects on the size-fecundity relationship in a common grasshopper across an aridity gradient.- *Journal of Orthoptera Research*, 17: 265-271.

Degen T., Hovestadt T., Mitesser O., Hölker F., 2015.- High female survival promotes evolution of protogyny and sexual conflict.- *PLoS ONE*, 10: e0118354.

Denno R. F., McClure M. S., Ott J. R., 1995.- Interspecific interactions in phytophagous insects: Competition reexamined and resurrected.- *Annual Review of Entomology*, 40: 297-331.

Fagerström T., Wiklund C., 1982.- Why do males emerge before females? Protandry as a mating strategy in male and female butterflies.- *Oecologia*, 52: 164-166.

Fairbairn D. J., 1997.- Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females.- *Annual Review of Ecology and Systematics*, 28: 659-687.

Firmino P. N., Calvão T., Ayres M. P., Pimentel C. S., 2017.- *Monochamus galloprovincialis* and *Bursaphelenchus xylophilus* life history in an area severely affected by pine wilt disease: implications for forest management.- *Forest Ecology and Management*, 389: 105-115.

Fischer K., Fiedler K., 2001.- Egg weight in the butterfly *Lycaena hippothoe*: more small or fewer large eggs?- *Population Ecology*, 43: 105-109.

Fox C. W., Stillwell R. C., Wallin W. G., Hitchcock L. J., 2006.- Temperature and host species affect nuptial gift size in a seed-feeding beetle.- *Functional Ecology*, 20: 1003-1011.

García-Barros E., 2000.- Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea).- *Biological Journal of the Linnean Society*, 70: 251-284.

Gillooly J. F., Charnov E. L., West G. B., Savage M., Brown J. H., 2002.- Effects of size and temperature on development time.- *Nature*, 417: 70-73.

Gu H.-F., Xiao J.-H., Dunn D. W., Niu L.-M., Wang B., Jia L.-Y., Huang D.-W., 2014.- Evidence for the circadian gene period as a proximate mechanism of protandry in a pollinating fig wasp.- *Biology Letters*, 10: 20130914.

Hendry A. P., Day T., Cooper A. B., 2001.- Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness.- *American Naturalist*, 157: 387-407.

Honek A., 1993.- Intraspecific variation in body size and fecundity in insects: a general relationship.- *Oikos*, 66: 483-492.

Honek A., 1997.- Incidence of protogynous and protandrous development in the pre-imaginal stage of insect development: an overview.- *Acta Societas Zoologicae Bohemicae*, 61: 113-128.

Horne C. R., Hirst A. G., Atkinson D., 2017.- Seasonal body size reductions with warming covary with major body size gradients in arthropod species.- *Proceedings of the Royal Society B: Biological Sciences*, 284: 20170238.

Hughes A. L., Hughes M. K., 1982.- Male size, mating success, and breeding habitat partitioning in the white spotted sawyer *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae).- *Oecologia*, 55: 258-263.

Hughes A. L., Hughes, M. K., 1987.- Asymmetric contests among sawyer beetles (Cerambycidae: *Monochamus notatus* and *Monochamus scutellatus*).- *Canadian Journal of Zoology*, 65: 823-827.

Jones M. E., Hanlon C. C., Paine T. D., 2015.- Potential for interspecific competition between congeneric longhorned beetle species (Coleoptera: Cerambycidae) in an adventive environment.- *Environmental Entomology*, 44: 960-965.

Kaplan I., Denno R. F., 2007.- Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory.- *Ecology Letters*, 10: 977-994.

Koutroumpa F. A., Vincent B., Roux-Morabito G., Martin C., Lieutier F., 2008.- Fecundity and larval development of *Monochamus galloprovincialis* (Coleoptera Cerambycidae) in experimental breeding.- *Annals of Forest Science*, 65: 707-718.

Koutroumpa F. A., Rougon D., Bertheau C., Lieutier F., Roux-Morabito G., 2013.- Evolutionary relationships within European *Monochamus* (Coleoptera: Cerambycidae) highlight the role of altitude in species delineation.- *Biological Journal of the Linnean Society*, 109: 354-376.

Lawton J. H., Strong D. R., 1981.- Community patterns and competition in folivorous insects.- *American Naturalist*, 118: 317-338.

Le Lagadec M. D., Chown S. L., Scholtz C. H., 1998.- Desiccation resistance and water balance in southern African keratin beetles (Coleoptera, Trogidae): the influence of body size and habitat.- *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, 168: 112-122.

Linsley E. G., Chemsak J. A., 1984.- *The Cerambycidae of North America, Part VII, No. 1: taxonomy and classification of the subfamily Lamiinae, tribes Parmenini through Acanthoderini*.- University of California Publications in Entomology, University of California Press, Berkeley and Los Angeles, California, USA.

Messina F. J., Peterson M., 2004.- Predictable modification of body size and competitive ability following a host shift by a seed beetle.- *Evolution*, 58: 2788-2797.

Miller D. R., Dodds K. J., Eglitis A., Fettig C. J., Hofstetter R. W., Langor D. W., Mayfield III A. E., Munson A., Poland T. M., Raffa K., 2013.- Trap lure blend of pine volatiles and bark beetle pheromones for *Monochamus* spp. (Coleoptera: Cerambycidae) in pine forests of Canada and the United States.- *Journal of Economic Entomology*, 106: 1684-1692.

Møller A. P., 2004.- Protandry, sexual selection and climate change.- *Global Change Biology*, 10: 2028-2035.

Morbey Y. E., 2013.- Protandry, sexual size dimorphism, and adaptive growth.- *Journal of Theoretical Biology*, 339: 93-99.

Parker G. A., Begon M., 1986.- Optimal egg size and clutch size: effects of environment and maternal phenotype.- *American Naturalist*, 128: 573-592.

Parry D., Goyer R. A., Lenhard G. J., 2001.- Macrogeographic clines in fecundity, reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma disstria*.- *Ecological Entomology*, 26: 281-291.

Pershing J. C., Linit M. J., 1986.- Biology of *Monochamus carolinensis* (Coleoptera: Cerambycidae) on Scotch pine in Missouri.- *Journal of the Kansas Entomological Society*, 59: 706-711.

Pimentel C., Ferreira C., Nilsson J.-Å., 2010.- Latitudinal gradients and the shaping of life-history traits in a gregarious caterpillar.- *Biological Journal of the Linnean Society*, 100: 224-236.

Pimentel C., Santos M., Ferreira C., Nilsson J.-Å., 2012.- Temperature, size, reproductive allocation, and life-history evolution in a gregarious caterpillar.- *Biological Journal of the Linnean Society*, 105: 340-349.

Pimentel C. S., Ayres M. P., Vallery E., Young C., Streett D. A., 2014.- Geographical variation in seasonality and life history of pine sawyer beetles *Monochamus* spp: its relation with phoresy by the pinewood nematode *Bursaphelenchus xylophilus*.- *Agricultural and Forest Entomology*, 16: 196-206.

Pincheira-Donoso D., Tregenza T., Butlin R. K., Hodgson D. J., 2018.- Sexes and species as rival units of niche saturation during community assembly.- *Global Ecology and Biogeography*, 27: 593-603.

Polis G. A., Myers C. A., Holt R. D., 1989.- The ecology and evolution of intraguild predation: potential competitors that eat each other.- *Annual Review of Ecology and Systematics*, 20: 297-330.

Roff D. A., 1992.- *The evolution of life histories, theory and analysis*.- Chapman and Hall, New York, USA.

Schoeller E. N., Husseneder C., Allison J. D., 2012.- Molecular evidence of facultative intraguild predation by *Monochamus titillator* larvae (Coleoptera: Cerambycidae) on members of the southern pine beetle guild.- *Naturwissenschaften*, 11: 913-924.

Scriven J. J., Whitehorn P. R., Goulson D., Tinsley M. C., 2016.- Bergmann's body size rule operates in facultatively endothermic insects: evidence from a complex of cryptic bumble bee species.- *PLoS ONE*, 11: e0163307.

Serrano-Meneses M. A., Córdoba-Aguilar A., Méndez V., Layen A. J., Székely T., 2007.- Sexual size dimorphism in the American ruby spot: male body size predicts male competition and mating success.- *Animal Behaviour*, 73: 987-997.

Shelomi M. 2012.- Where are we now? Bergmann's rule *sensu lato* in insects.- *American Naturalist*, 180: 511-519.

Stillwell R. C., Morse G. E., Fox C. W., 2007.- Geographic variation in body size and sexual size of a seed-feeding beetle.- *American Naturalist*, 170: 358-369.

Stillwell R. C., Blanckenhorn W. U., Teder T., Davidowitz G., Fox C. W., 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.

Teder T., 2014.- Sexual size dimorphism requires a corresponding sex difference in development time: a meta-analysis in insects.- *Functional Ecology*, 28: 479-486.

Teder T., Tammaru T., 2005.- Sexual size dimorphism within species increases with body size in insects.- *Oikos*, 108: 321-334.

Tomminen J., 1993.- Development of *Monochamus galloprovincialis* Olivier (Coleoptera, Cerambycidae) in cut trees of young pines (*Pinus sylvestris* L.) and log bolts in southern Finland.- *Entomologica Fennica*, 4: 137-142.

Weir L. K., Grant J. W., Hutchings J. A., 2011.- The influence of operational sex ratio on the intensity of competition for mates.- *American Naturalist*, 177: 167-176.

Werner E. E., Gilliam J. F., 1984.- The ontogenetic niche and species interactions in size-structured populations.- *Annual Review of Ecology and Systematics*, 15: 393-425.

Wissinger S. A., 1992.- Niche overlap and the potential for competition and intraguild predation between size-structured populations.- *Ecology*, 73: 1431-1444.

Zonneveld C., Metz J., 1991.- Models on butterfly protandry: virgin females are at risk to die.- *Theoretical Population Biology*, 40: 308-321.

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