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Ecophysiological Determinants of Sexual Size Dimorphism: Integrating Growth Trajectories, Environmental Conditions, and Metabolic Rates

Marie-Claire Chelini, John P. Delong, and Eileen A. Hebets

Abstract

Sexual size dimorphism (SSD) often results in dramatic differences in body size between females and males. Despite its ecological importance, little is known about the relationship between developmental, physiological, and energetic mechanisms underlying SSD. We take an integrative approach to understand the relationship between developmental trajectories, metabolism, and environmental conditions resulting in extreme female-biased SSD in the crab spider *Mecaphesa celer* (Thomisidae). We tested for sexual differences in growth trajectories, as well as in the energetics of growth, hypothesizing that female *M. celer* have lower metabolic rates than males or higher energy assimilation. We also hypothesized that the environment in which spiderlings develop influences the degree of SSD of a population. We tracked growth and resting metabolic rates of female and male spiderlings throughout their ontogeny and quantified the adult size of individuals raised in a combination of two diet and two temperature treatments. We show that *M. celer*'s SSD results from differences in the shape of female and male growth trajectories. While female and male resting metabolic rates did not differ, diet, temperature, and their interaction influenced body size through an interactive effect with sex, with females being more sensitive to the environment than males. We demonstrate that the shape of the growth curve is an important but often overlooked determinant of SSD and that females may achieve larger sizes through a combination of high food ingestion and low activity levels. Our results highlight the need for new models of SSD based on ontogeny, ecology, and behavior.

Keywords Growth trajectories, Ontogeny, SSD, Temperature-size rule, Thomisidae

Introduction

Body size is one of the most important traits of any organism, as it influences processes ranging from intracellular reactions to community structure and dynamics (Savage et al. 2004; Gillooly et al. 2005; Brose et al. 2006; Riede et al. 2011; DeLong et al. 2015). In species with sexual size dimorphism (SSD), body size and all processes associated with it can vary widely between the sexes. Fitness benefits associated with different body sizes in females and males have been studied in depth in a wide range of taxa, from mammals to insects (Blanckenhorn 2000, 2005; Preziosi and Fairbairn 2000; Cox and Calsbeek 2009). Understanding the evolution of SSD, however, depends on determining how these dimorphic organisms reach drastically different sizes at adulthood despite sharing a similar physiology and autosomal genomes (Fairbairn 1997; Badyaev 2002a; Teder 2014; Chou et al. 2016).

The proximate mechanisms of SSD—i.e. its developmental, energetic, behavioral, and physiological basis—have typically been studied from one of two primary perspectives: (1) comparing developmental growth trajectories (i.e. ontogeny) of females and males or (2) focusing on individual-level energy budgets, comparing foraging rates and energetic expenditure of females and males. These two perspectives are, however, fundamentally interrelated: If growth trajectories differ, how does the larger sex fuel its faster or longer growth? Rather than solving the proximate

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basis of SSD, focusing on a single one of these perspectives in isolation leads to inevitably partial and biased, if not possibly wrong, answers.

From an ontogenetic standpoint, SSD is achieved through differences in growth trajectories: sexes may be born at different sizes, one sex may grow for longer than the other, or one sex may grow faster than the other (Leigh and Shea 1996; Badyaev 2002a; Blanckenhorn et al. 2007; Stillwell et al. 2010; Teder 2014). Differences in egg size or size at birth are extremely rare in arthropods (Stillwell et al. 2010; Teder 2014; but see Budrienė et al. 2013) but have been observed in birds (Weatherhead and Teather 1994) and mammals (Ono and Boness 1996; Smith and Leigh 1998). The difference in size at birth is, however, seldom proportional to the degree of SSD reached at adulthood (Weatherhead and Teather 1994; Badyaev 2002a). In contrast to differences in size at birth, differences in growth duration, growth rate, and a combination of both are all common in sexually size dimorphic mammals (Smith and Leigh 1998; Badyaev 2002a; Garel et al. 2006; O'Mara et al. 2012), reptiles (Shine 1994) and a vast number of arthropods (Blanckenhorn et al. 2007; Stillwell and Davidowitz 2010; Teder 2014). Truly understanding the growth trajectory underlying SSD requires, however, a detailed analysis of the entire development of both sexes. Indeed, quantifying the relationship between size at adulthood and duration of development cannot uncover periods of sex-specific increased growth. Such life-long analyses of growth patterns across sexes are scarce, presumably due to the logistical difficulties involved in following daily the growth of large numbers of individuals of both sexes for extensive periods of time (but see Vendl et al. 2016, 2018; Rohner et al. 2017, 2018).

If SSD results from differences in the growth trajectory of females and males, we might expect that the two sexes will also differ in their allocation of energy to growth and maintenance. Indeed, life history theory predicts energetic trade-offs between growth, maintenance, and reproduction (Stearns 1976, 1989). The energy available for growth depends on an individual's energy intake (foraging) and on the energy spent maintaining its existing tissues (i.e. its resting metabolic rate) and fueling activity (Hou et al. 2008; Dmitriew 2011). As such, in species with marked degrees of SSD, the larger sex may achieve its faster/longer growth by reducing its expenditure and using the savings to further growth and/or by increasing its food energy intake (Shine 1989; Holtby and Healey 1990; Ono and Boness 1996; Isaac 2005; Mikolajewski et al. 2005; Fuselier et al. 2007; Rennie et al. 2008). In other words, in species with SSD driven by differences in growth trajectories, we expect the sexes to also differ in a couple of possible ways: (1) the larger sex has a lower overall energetic expenditure than the smaller sex and/or, (2)

the larger sex has a higher foraging rate than the smaller sex.

Finally, in addition to looking at the interrelatedness of growth trajectories and energetics, it is important to also take into account the environmental context in which organisms are growing when determining the proximate basis of SSD (Teder and Tammaru 2005). Indeed, temperature and seasonality may greatly influence growth rate, development time, and resting metabolic rates within a species. Differences in seasonal timing or geographic location may lead to variation in the growth trajectory and metabolism of each sex and, consequently, to variation in a species' degree of SSD (Badyaev 2002b; Stillwell and Davidowitz 2010; Auer et al. 2015; Rohner et al. 2018). In addition, as temperature influences metabolic rates and diet influences the amount of energy an individual has to allocate to both growth and tissue maintenance, understanding the interactive effect of both temperature and diet on female and male adult sizes sheds light into the metabolic basis of SSD.

In this study, we explore the proximate mechanisms of SSD by quantifying changes in growth trajectories and metabolic rates among males and females of the extremely sexually dimorphic crab spider *Mecaphesa celer*. We also assess the effects of varying regimes of diet and temperature on their size at adulthood. Specifically, we (1) test for sexual differences in developmental time, growth rate, and the shape of growth trajectories of each instar of females and males to reveal the detailed ontogeny of SSD; (2) determine how females and males differ in the energetics of their growth, hypothesizing that female *M. celer* have a lower metabolic rate than males—i.e., they devote less energy to their tissue maintenance, saving more energy to growth. Alternatively, (3) we hypothesize that female and male *M. celer* differ in their assimilation of energy, with females having a higher food intake than males, in which case we predict that food restriction has a stronger effect on females than males. Finally, (4) we test the hypothesis that the environment in which individuals grow will influence the population-level degree of SSD by raising spiderlings in two different temperature treatments.

Material and Methods

Study system

Spiders offer an ideal system with which to study the mechanisms underlying size differences between females and males as extreme degrees of SSD, mostly female biased, have evolved multiple times within the group (Scharff and Coddington 1997; Hormiga et al. 2000; Legrand and Morse 2000). Here, we use the crab spider *Mecaphesa celer* (Hentz 1847) as a model system

to understand the proximate mechanisms of SSD. Crab spiders (family Thomisidae) comprise some of the most extremely dimorphic spider species (Foellmer and Moya-Larano 2007). Female *M. celer* are 1.3–2 times the body size of males (measured either as cephalothorax width or total body length), but often weigh more than 10 times the average male mass. Several crab spider species, including *M. celer*, are protandric, meaning that males mature earlier than females (Muniappan and Chada 1970; Dodson and Beck 1993; Morse 2013; Chelini and Hebets 2017). The degree of SSD reached at adulthood is not, however, proportional to the observed differences in growth length—females double in size in their last three instars, but mature only a few days after males (Muniappan and Chada 1970; Chelini and Hebets 2017). When and how SSD arises remain unanswered questions in such extremely dimorphic organisms, requiring a thorough analysis of the entire ontogeny of females and males.

Growth trajectories

To test the hypothesis that differences in growth trajectories underlie SSD in *M. celer*, we followed the growth of 250 *M. celer* spiderlings beginning at their second instar (first-instar spiderlings are extremely small and fragile, and remain aggregated around the egg sac until their first molt). These spiderlings were born in the laboratory between September and October 2014. They were the offspring of 48 females collected in Lincoln, Nebraska, USA in May 2014 and mated in the laboratory in August 2014. We randomly selected 5–10 spiderlings from each clutch and housed them in individual 4 × 4 × 6 cm acrylic boxes, with ad libitum water, and small pieces of netting for perching, in a room at 26 °C and 60% relative humidity, under a 14:10 light:dark cycle. We checked all spiderlings for molts three times a week. After each molt, we photographed each spiderling with a Spot Flex® digital camera (Model 15.2 64 MP, Diagnostic Instruments, Inc.) mounted on a Leica® DM 4000 B Microscope. We fed all individuals twice a week with flightless *Drosophila melanogaster* in quantities corresponding to each spiderling's age: third instar spiderlings were fed three *D. melanogaster*, fourth instar spiderlings were fed four *D. melanogaster*, etc. (as a reference, third instar *M. celer* spiderlings are approximately twice the size of one *D. melanogaster*). This food regime allowed us to progressively increase how much food was available to each spiderling as they aged, while being kept constant across cohorts of spiderlings of the same instar and of both sexes. We used all individuals that successfully reached adulthood (N = 43 females and 35 males) for size and growth quantifications. As spiderling sex can only be identified at their fifth instar, our sample size was limited by the high mortality rates of early instar spiderlings whose sex was unknown.

We measured the cephalothorax width of each spiderling at each of their developmental instars from the photographs taken after their molts with ImageJ (Rasband 1997–2012). Cephalothorax width is the most recommended proxy for body size in spiders, as it remains fixed between molts and after sexual maturation and does not change with the physiological state of the spider (Prenter et al. 1995; Foellmer and Moya-Larano 2007; Foelix 2011). Linear measurements of body size, such as cephalothorax width, are nonetheless strongly correlated to mass in *M. celer* (Muniappan and Chada 1970, see also Online Resource 1 for a graphical comparison of mass vs. cephalothorax width change with spiderling age). We calculated spiderling age in days after birth and kept track of the date (± 2 days) and number of their molts, which allowed us to determine the average length, in days and in instars, of each individual's development.

We tested for differences in female and male growth trajectories using two Gamma Generalized Linear Mixed Models (GLMMs) with a log link. In one model, we used the size (cephalothorax width) of each spiderling at each instar as the response variable, instar and sex as predictor variables, and the family ID/spiderling ID as a random effect. In a second model, we replaced the instar by their age in days. Gamma distributions were more appropriate than the linear distributions for our growth trajectory models as spiderling sizes were not normally distributed, but right skewed and heteroskedastic (Bolker et al. 2009). We ran these analyses in R v3.01, using the function glmer from the package lme4 (R Core Team 2014; Bates et al. 2015).

Energetics of growth: metabolic rate measurements

To test the hypothesis that females have a lower energetic expenditure at rest than males throughout their ontogeny, we measured the oxygen consumption rate of 146 of the spiderlings described above using an OXY-10 micro fluorescent oxygen sensor (PreSens, Regensburg, Germany). Prior to each measurement, we calibrated our oxygen sensors to 0% and 100% O_2 concentrations using vials of pure N_2 and pure O_2, respectively. To ensure that oxygen consumption measurements were for resting spiders, we placed each spiderling at the bottom of a 0.5 ml Eppendorf® microcentrifuge tube and held them in place by a circular 2.5 mm diameter piece of netting (allowing oxygen flow but reducing spiderling movement). We then placed these microcentrifuge tubes in a thermocycler at 26 °C, where spiderlings acclimated for 30 min before we started recording their oxygen consumption. The oxygen sensors were carefully inserted through a small hole in the cap of the Eppendorf tube, which was subsequently sealed. We checked that these tubes did not leak oxygen by placing oxygen sensors in empty tubes and verifying that the oxygen levels inside the tubes

remained constant in the absence of a spiderling. We recorded spiderling oxygen consumption for periods of approximately 50 min (post-acclimation). We recorded oxygen consumption for a relatively long period of time to ensure that we would have an accurate estimate of the smaller spiderlings' metabolic rate. We then kept this recording length across all developmental instars for consistency's sake.

We calculated the metabolic rate of each spiderling as the slope of the linear regression between mass of oxygen inside the Eppendorf® tubes against time (mg O_2/min). To avoid including periods of spiderling stress, movement, and for consistency across measurement, we used only the shallowest segment of each spiderling's oxygen consumption slope for our estimate of resting metabolic rate. To avoid potential biases due to stress, we used the longest possible shallow segments, which varied between 20 and 45 min. This makes our measurements of respiration rates conservative. Spiderlings typically settled on the side of the vials within minutes and moved very little afterward. To avoid quantifying the metabolic costs of digestion and molting, we controlled the timing of our measurements: we measured metabolic rates 2 days after a feeding day and between 1 and 3 weeks following their previous molt (instars vary in length from five to 80 days—Muniappan and Chada 1970). We randomly selected 10–20 individuals of each sex to be tested at each instar, with no individual being used more than once.

We weighed each spiderling to the nearest 0.1 mg immediately after measuring their metabolic rates using an Ohaus® precision scale. Data on oxygen consumption rate and mass were log transformed to linearize the relationship between metabolic rates and size/mass. We used a linear mixed model (LMM) to determine the relationship between resting metabolic rate and each sex's mass, using the natural log of the resting metabolic rate as our response variable, sex, natural log of mass, and their interaction as predictor variables, and spiderling family as a random effect. We then conducted a likelihood ratio test between this full model, a model with log of mass as the sole predictor variable, and a null model. We ran these analyses using the function lmer from R's package lme4 and the function anova (R Core Team 2014; Bates et al. 2015).

Environmental effects on SSD: diet and temperature manipulation

To determine the effects of diet and temperature on the degree of SSD of *M. celer*, we subjected 1000 spiderlings to four treatments in a 2 × 2 factorial design involving two diet treatments (High diet vs. Low diet) and two temperature treatments (Warm vs. Cool—Table 1). All spiderlings were born in the laboratory, resulting from the same pairings described in *Growth trajectories* (above). Siblings were equally distributed among all treatments. The Warm treatment was identical to the environmental conditions described above (see *Growth trajectories*). Spiderlings from the Cool treatment were reared at temperatures averaging 18 °C, with ± 5 °C fluctuations in temperature. We aimed at rearing the spiderlings in the Cool treatment at 18 °C through their entire development, but construction in the building and issues with the heating system made it impossible for us to keep this temperature constant. As such, the experiment began with spiderlings being born in a room at 26 °C (October), being moved to a room at 18 °C (November–December), which was subsequently cooled down to 13 °C (January–April), then warmed up again to 16 °C (May–June), 18 °C (July–August), and finally to 20 °C, with mild oscillations in temperature (± 5 °C) occurring during each of these "seasons" and lasting from 1 to 3 days. We used a 14:10 light:dark cycle for all treatments. High diet spiderlings were fed with flightless *D. melanogaster* according to the schedule described in *Growth trajectories*, in quantities corresponding to each spiderling age, twice a week. Low diet spiderlings were fed the same diet, but only once a week. The spiderlings used in our analyses of *Growth trajectories* and *Energetics of growth* were the same as those of our High diet—Warm treatment. Sexually mature spiders (recognizable by developed pedipalp embolus in males and open genital operculum in females) were then photographed and measured following the same methods used for spiderlings (see *Growth trajectories* for details).

We tested for an effect of diet and temperature on the degree of SSD in *M. celer* with a linear model (LM), with diet, temperature, sex, and their interaction as predictor variables of the size (cephalothorax width) at adulthood. We ran these analyses using the function *lm* from R's package *lme4* (R Core Team 2014; Bates et al. 2015).

Table 1. Summary of the diet and temperature treatments used to test the effects of the environment on the sexual size dimorphism of *Mecaphesa celer*

High diet Warm (HW)
26 °C, *D. melanogaster*
  2 × per week
n = 250
High diet Cool (HC)
~18 °C (±5 °C), *D. melanogaster* 2 × per week
n = 250

Low diet Warm (LW)
26 °C, *D. melanogaster*
  1 × per week
n = 250
Low diet Cool (LC)
~18 °C (±5 °C), *D. melanogaster* 1 × per week
n = 250
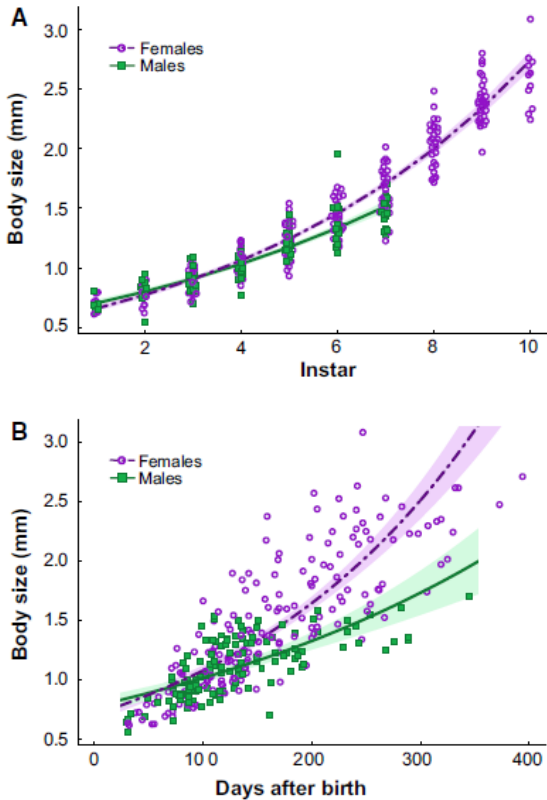
Figure 1. Growth trajectories of female and male *Mecaphesa celer*. **a** Body size (cephalothorax width) per instar, **b** body size (cephalothorax width) per day after birth. Females have two to four developmental instars more than males, but also grow faster. Lines represent the best fit of a Gamma GLMM and shaded areas represent the 95% confidence interval

Table 2. Gamma GLMM testing the relation between *Mecaphesa celer* size (cephalothorax width) at each developmental instar and sex

	Estimate	St. error	t	p
Intercept	− 0.57	0.03	− 21.67	< 0.001
Instar	0.16	0.003	61.25	< 0.001
Sex (M vs. F)	0.10	0.04	2.68	0.007
Instar * sex	− 0.03	0.005	− 6.03	< 0.001

$N = 304$, deviance = − 526.2, random effect variance: spiderling ID: family = 0.002, st. dev. = 0.05, family = 0.0003, st. dev. = 0.01; likelihood ratio test: $\chi^2 = 848.8$, $df = 3$, $p < 0.001$

Table 3. Gamma GLMM testing the relation between *Mecaphesa celer* size (cephalothorax width), age in days and sex

	Estimate	St. error	t	p
Intercept	− 0.45	0.05	− 8.99	< 0.001
Age (days)	0.005	0.0001	35.57	< 0.001
Sex (F vs. M)	0.13	0.07	1.95	0.05
Age * sex	0.002	0.0002	− 6.40	< 0.001

$N = 304$, deviance = − 216.19; random effect variance: spiderling ID: family = 0.01, st. dev. = 0.1, family = 0.001, st. dev. = 0.04; Likelihood ratio test: $\chi^2 = 539.32$, $df = 3$, $p < 0.001$
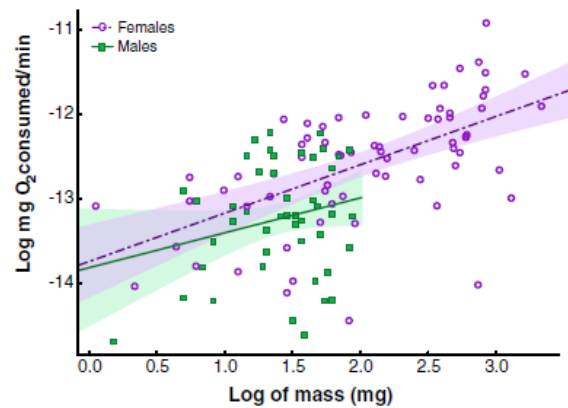
Figure 2. Resting metabolic rate scaling with mass of both female and male *Mecaphesa celer* at different points of their ontogeny. Lines represent the best fit of a linear model and shaded areas represent the 95% confidence interval
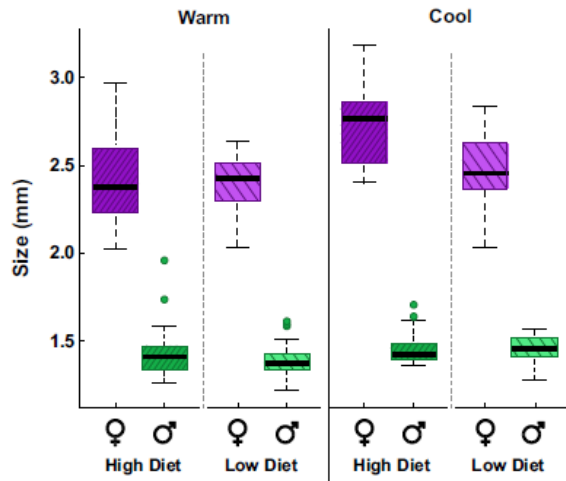
Results

Growth trajectories

Female and male *M. celer* growth trajectories differed in both length and shape (Figure 1). Females matured in eight (N = 14), nine (N = 18) or ten instars (N = 11), while males matured in six (N = 16) or seven instars (N = 18). Females reached maturity in an average of 273.7 days (min = 102, max = 394), while males took on an average 204 days (min = 109, max = 345). Females and males differed significantly in the size (cephalothorax width) from the fifth instar onward (Table 2, non-overlapping confidence intervals in Figure 1), as well as in the relationship between size and age in days (Table 3; Figure 2).

Energetic demand quantification: metabolic rate measurements

Mecaphesa celer's resting metabolic rate scaled with mass with a slope of 0.57. Contrary to our predictions, neither the slope nor the intercept of the mass-resting metabolic rate relationship differed between females and males (Likelihood ratio test of models with and without the variable "sex": $X^2 = 1.33$, p = 0.51, Table 4, Figure 3).

Table 4. LMM testing the effect of log of mass (mg), sex, and their interaction on the resting metabolic rate (mg O_2 consumed/min) of *Mecaphesa celer* spiders along their ontogeny

	Estimate	St. error	t	p
Intercept	− 13.72	0.21	− 64.22	< 0.001
Sex	− 0.08	0.41	− 0.19	0.85
Log mass	0.57	0.10	5.79	< 0.001
Sex * log mass	− 0.16	0.26	− 0.61	0.55

Spiderling families were used as random effect. χ^2 = 44.85, *df* = 3, *p* = 9.98e−10

Table 5. Linear model testing the effect of diet, temperature, sex, and their interaction on the size (cephalothorax width) of adult *Mecaphesa celer* spiders

	Estimate	St. error	t	p
Intercept	2.71	0.04	66.17	< 0.001
Sex (M vs. F)	− 1.25	0.05	− 23.49	< 0.001
Diet (high vs. low)	− 0.24	0.05	− 4.63	< 0.001
Temperature (warm vs. cool)	− 0.30	0.05	− 6.39	< 0.001
Sex * diet	0.23	0.07	3.23	0.001
Sex * temperature	0.28	0.06	4.29	< 0.001
Diet * temperature	0.24	0.06	3.65	< 0.001
Sex * diet * temperature	− 0.27	0.09	− 3.02	0.003

Multiple *R*-squared: 0.91, *R*-squared: 0.91, *F* = 342.2, *df* = 226, *p* ≤ 0.001

Figure 3. Size (cephalothorax width) of adult female and male *Mecaphesa celer* in two diet and temperature treatments. Boxes correspond to first quartile, median and third quartile, whiskers correspond to the range (not including outliers, which are represented by points). Females are represented by purple and males by green, and the boxes' pattern matches the diet treatment (narrow stripes for high diet, wide stripes for low diet) (color figure online)

Environmental effects on SSD: diet and temperature manipulation

Diet, temperature, and their interaction affected *M. celer* size (Table 5). Individuals in the High diet–Cool (HC) treatment achieved the largest sizes of all treatments, while individuals in the LW treatment achieved the smallest sizes (Table 5; Figure 3). Females in the HC diet were on average 12% larger than females in the LW treatment, while HW males were just 6% larger than LW males. Females were larger than males, with no overlap in size distribution, in all treatments (Figure 3). Female size had a larger variance than male size both within and between treatments (Figure 3).

Discussion

Understanding the ontogenetic, energetic, and environmental determinants of SSD is paramount to understanding the ecology and evolution of sexually dimorphic species. Such an understanding is, however, still currently lacking. Using an integrative approach, here we show that the shape of females' growth curve is the main developmental mechanism of SSD in this species. Surprisingly, *Mecaphesa celer* females' faster and longer growth seems unrelated to either sex' mass-specific resting metabolic rate. Also, the energy available to each sex (diet treatments) had only a modest effect on the size obtained by both females and males at adulthood, and was influenced through an interactive effect with temperature. Both temperature and diet had a stronger effect on adult female size than on male size.

Growth trajectories

Females do not grow faster than males throughout their entire ontogeny, but rather grow faster only from their fifth instar on. The non-linear shape of the growth trajectory at the basis of the observed differences is, therefore, only visible after the appearance of the external secondary sexual characters of these animals. The simultaneous appearance of secondary sexual characters and sexual size dimorphism suggests an endocrine basis to differences in growth rate observed between the sexes from their fifth instar onward (see Cox et al. 2005). This is consistent with the results of Trabalon and Blais (2012) showing an increase in the arthropod hormone ecdysteroid in males, one instar prior to adulthood, concomitantly with a differentiation of females' and males' growth rates and the appearance of secondary sexual traits.

The role of the functional form of the growth trajectory cannot be observed if growth rate is determined

simply as the static relationship between size at adulthood and development time. Erroneously assuming that SSD is caused by linear differences in growth rate or differences in development time makes it impossible to correctly identify the target of selection: growth rate, developmental time, or shape of the growth curve (Tammaru and Esperk 2007; Tammaru et al. 2010; Vendl et al. 2018). Our results, thus, stress the need for long-term experiments to get a complete picture of the processes that lead to SSD.

Energetics of growth

Most models of ontogenetic growth predict a relationship between growth rate, the amount of energy ingested, and the cost of maintaining an organism's existing tissues (e.g. West et al. 2001; Ricklefs 2003; Moses et al. 2008; Hou et al. 2008; DeLong 2012). As such, it is surprising that females and males raised in identical conditions reach drastically different sizes despite having virtually identical resting metabolic rates throughout their ontogeny. Females are nonetheless growing faster than males, and, as such, must obtain the fuel for this growth from somewhere, either through reduced energetic expenditure, or through increased energetic intake (Dmitriew 2011).

Differences in energetic expenditure

Sex-specific levels of energetic expenditure could be related to each sex's active metabolic rate (i.e. metabolic rates reached during activity) rather than resting metabolic rate (Gade 2002; Downs et al. 2016). Differences between active and resting metabolic rates between females and males have not been observed in spiders (Shillington and Peterson 2002), but this hypothesis should nonetheless be tested.

Differences in behavior also may result in sex-specific energetic expenditures. In multiple sexually size dimorphic species, females and males differ in their activity levels and overall life history (Vollrath and Parker 1992; Vollrath 1998; Beck et al. 2007; Tammaru et al. 2010; Rohner et al. 2017)—e.g., the larger sex is often less mobile than the smaller sex (González-Solís et al. 2000; Mikolajewski et al. 2005; Dodson et al. 2015; but see Rennie et al. 2008). In spiders, adult females of the most extremely SSD species, including *M. celer*, are highly specialized sit-and-wait predators, while males typically spend their adult instar roaming in search of females (Walker and Rypstra 2001, 2002; Foellmer and Moya-Larano 2007; Dodson et al. 2015). As a consequence, females could fuel their faster growth simply by being less active than males, allowing them to allocate more of their available energy to growth. To test this hypothesis, we would have to assess if differences in activity levels between females and males extend from early instars to adulthood.

Most studies on life history divergence between the sexes focus solely on adults, unfortunately. Nonetheless, this behavioral difference is a likely explanation for our observed differences in growth trajectory with no underlying difference in female and male metabolic rates, and, upon being corroborated, could be considered a novel mechanism of sexual size dimorphism. From an evolutionary standpoint, the increased activity of males may lead to an increased mortality risk, which would select for smaller, inconspicuous, and rapidly maturing males (Blanckenhorn 2000).

Differences in energetic intake

Alternatively, or in addition to differences in activity levels, SSD may be proximately caused by differences in the energy assimilated by each sex. In other words, the larger sex may forage more efficiently throughout their development than the smaller sex (Shine 1989; Rohner et al. 2018). Foraging is, however, in and of itself an energetically costly process that scales with predator size (Tenhumberg et al. 2000; Carbone et al. 2007). Smaller organisms reach satiation faster and may, therefore, minimize their foraging effort regardless of how much food is available in the wild. Such a reduction in foraging effort allows for more time and energy to be spent in reproductive activities (Blanckenhorn et al. 1995; Blanckenhorn and Viele 1999; Blanckenhorn 2005). In a sex for which there are no benefits associated with being large (i.e. male *M. celer*, see Chelini and Hebets 2016), optimal size might, therefore, be selected by the temporal and energetic benefits of being small, and might remain relatively fixed regardless of the foraging conditions under which males grow (Shine 1989; Blanckenhorn 2000). Females, on the other hand, are likely to be under selection for larger sizes and maximized food consumption due to the fecundity benefits associated with size (Richard Shine 1988; Honěk and Honek 1993; Preziosi et al. 1996). Indeed, in multiple orders of insects, female growth is known to be more sensitive to environmental conditions than male growth (Teder and Tammaru 2005).

Our results fit this pattern, as diet had a stronger effect on female size than on male size. The fact that all treatments have similar degrees of sexual size dimorphism demonstrates that differential food access is not the limiting factor of male size, but indicates that differences in actual energetic assimilation underlie the growth rates of female and male *M. celer*. In the wild, female sit-and-wait foraging strategy likely minimizes the energetic cost of foraging (Norberg 1977; Anderson and Karasov 1981). Moreover, females are likely to have access to larger and more energetically rewarding prey items than males, as a positive feedback generated from obtaining larger size (see Holtby and Healey 1990; González-Solís et al. 2000; Brose et al. 2006; Brose

2010, for examples, on size-dependent sex-specific foraging strategies in mammals and fish). It is, therefore, possible that extreme degrees of SSD may be proximately caused by differences in the foraging efficiency of females and males throughout their development, with the larger sex presenting a foraging behavior that combines higher energetic assimilation through access to larger prey items and lower energetic demands due to lower activity.

Environmental effects on SSD

Individuals in the High diet–Cool treatment reached the largest sizes among our four treatments. The negative effect of warm temperatures on *M. celer*'s body size is in accordance with the temperature-size rule, which predicts that ectotherms will develop for longer and reach larger sizes at lower temperatures (Atkinson 1994; Forster and Hirst 2012). Metabolic rates are known to increase with temperature (Gillooly et al. 2001; Schmalhofer 2011), thus individuals from the Cool treatment must have lower metabolic rates throughout their ontogeny than individuals from the Warm treatments. A lower metabolic rate would, in turn, allow these Cool individuals to invest more of their energetic supply toward growth than those of Warm treatments, resulting in larger adults. We must, however, consider the fact that, due to factors outside of our control, the effect of cooler temperatures in our treatments is confounded with the effect of fluctuating temperatures. Our Cool treatments were consistently cooler than the Warm treatments, and differed on average by 8 °C, a major difference bound to have effects on the development of *M. celer*. Nonetheless, our experiment demonstrates clearly that the environment has an effect on the adult size of both males and females, and consequently that the degree of SSD is dependent on environmental conditions, corroborating our hypothesis. Growth is known to be plastic in many arthropods, varying according to temperature, diet, days between feeding events, photoperiod, among others (Teder and Tammaru 2005; Stillwell et al. 2010; Dmitriew 2011; Hirst et al. 2015). Other animals such as salmonids have been shown to regulate their metabolic rates according to food availability, allowing individuals to maximize their growth even in conditions where food was limited (Auer et al. 2015). In our results, the interactive effect between diet and temperature on body size suggests that the balance between energy acquisition and energy expenditure that leads to SSD greatly depends on environmental conditions. The fact that the environment had a stronger effect in females than males fits with what is known in other arthropods, as the larger sex is known to be more plastic in multiple orders of holometabolous insects (Teder and Tammaru 2005; Rohner et al. 2018). Interactive effects of sex-specific plasticity, diet, and temperature

may contribute to intraspecific variation in magnitude of SSD observed in many animal species distributed across a wide geographic and environmental range.

Conclusions

Our results highlight the importance of analyzing the entire ontogeny of a species to fully understand the developmental basis of SSD. We revealed that differences in growth rate are not constant throughout *M. celer*'s ontogeny, nor linear, and suggest an endocrine basis to the observed differences. Also, differences in resting metabolic rates do not underlie SSD in this species, suggesting that females achieve a higher growth rate through a combination of increased energy assimilation and decreased energy expenditure compatible with a sit-and-wait foraging strategy, which represents a compromise between the classical competing models of SSD development: higher energy acquisition or lower energy expenditure. Our results further suggest the possibility of a new mechanism of SSD driven by differences in energy expenditure through behavior. As we gain a better understanding of the growth trajectories leading to SSD, we must take into account the ontogenetic differences between the sexes and develop new theoretical models predicting the relation between metabolism and growth to fully understand the evolution of SSD. As for empirical studies, our research shows that crab spiders are an excellent subject for studies on the development of SSD and growth physiology in arthropods.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.
Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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