Developmental plasticity in metabolic rates reinforces morphological plasticity in response to social cues of sexual selection

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ABSTRACT

Developmental plasticity allows individuals to match their phenotype to the competitive environment they are most likely to encounter. Although there are numerous studies that demonstrate adaptive shifts in life-history and metric traits, we still have a poor understanding of whether internal physiological processes demonstrate plasticity and whether this plasticity supports life-history and metric traits. Here we use the Australian redback spider (*Latrodectus hasselti*), a species that demonstrates adaptive developmental shifts in response to the availability of females and the density of males, to examine the relationship between the routine metabolic rate (RMR) and the expression of size, body-condition and development rate. We reared immature males in three diet treatments, and in social environments that varied the presence/absence of females and the density of males and measured their RMR, weight, size and developmental rate at maturity. We show that although RMR decreased with decreasing resource abundance, RMR was positively correlated with the density of rivals. Moreover, RMR was not correlated with size or body-condition at maturity. Our results demonstrate that plasticity in the RMR supports plasticity in metric and life-history traits to create an integrated phenotype that matches the competitive environment.

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1. Introduction

Developmental plasticity allows individuals to increase their fitness by matching their phenotype to the specific competitive challenge they will encounter at maturity (Pigliucci, 2001; West-Eberhard, 2003). To date, we have a thorough understanding of the effects of temperature, photoperiod and predator presence on developmental tactics (Adler and Harvell, 1990; Benard, 2004; Nylin and Gotthard, 1998) and are also gaining insight into how social cues trigger developmental shifts (Kasumovic and Brooks, 2011). Our understanding of the various traits that these environmental triggers affect, however, is often limited to easily measured life-history and metric traits. As a result, we have a solid understanding of how traits such as size, weight or development time vary in response to environmental triggers (Pigliucci, 2001; West-Eberhard, 2003), but have a relatively poorer understanding of whether internal systems and regulatory processes respond in a similar manner.

The few studies examining plasticity in internal processes demonstrate that they also match their competitive environment. For example, the earlier maturity seen in wood frog tadpoles (*Rana sylvatica*) tadpoles in the presence of predators is accompanied by an increase in the rows of teeth and intestinal elongation that allows individuals to process resources more quickly (Relyea and Auld, 2004, 2005). Having internal systems that complement or support the external phenotypes is likely common, but their inconspicuous nature makes them more difficult to detect and characterize. In addition, it is often difficult to predict how external and internal phenotypes should complement one another and how each should respond to a particular environmental factor.

Variable social environments provide a unique opportunity to examine plasticity in external and internal processes. Male and female density and the quality of conspecifics in the local environment is already known to trigger adaptive developmental shifts in both metric and life-history traits (Kasumovic and Brooks, 2011). There is evidence that metabolic rate should do the same. For example, metabolic rates are correlated with functions critical to fitness such as dominance (Metcalfe et al., 1985; Røskaft et al., 1986) and costly mate attraction displays (Stoddard and Salazar, 2010). The correlation of metabolic rates with fitness, however, depends on the competitive context (Fischer et al., 2009; Hawkins

et al., 1968; Schaefer and Walters, 2010) (reviewed in Burton et al., 2011). As a result, individuals that shift their metabolic rate to match the context they are most likely to encounter may be favored.

Australian redback spiders (*Latrodectus hasselti*) offer an excellent opportunity to examine the effect of the social environment on whole-organismal developmental plasticity for two reasons. First, pheromones provide information on the availability of mates and the density of rivals (Andrade and Kasumovic, 2005; Kasumovic and Andrade, 2004; Kasumovic et al., 2009b), which triggers plastic allocation strategies (Kasumovic and Andrade, 2006). When reared in the presence of mature virgin females, redback males sacrifice size and body-condition to mature earlier (Kasumovic and Andrade, 2006). This allows males to reach females sooner and outcompete rivals due to first male sperm precedence (Kasumovic and Andrade, 2009; Snow and Andrade, 2005). In contrast, when virgin females are scarce and rivals are abundant, males prolong their development and mature larger and in better body-condition (Kasumovic and Andrade, 2006; Kasumovic et al., 2009a). Larger size increases mating success via female choice (Stoltz et al., 2009) while increased body-condition provides greater energetic reserves for mate searching and the prolonged competitive courtship needed against rivals required to gain access to females (Stoltz and Andrade, 2010).

Second, the density of available females and rival males is likely to change a male's lifetime energetic demands. For example, the particularly low metabolic rates of spiders (Anderson, 1970) may be important when females are rare as it would allow males to minimize energetic consumption, prolonging survival until females are found (e.g., Kasumovic et al., 2009a). This is especially advantageous for male web-building spiders as they leave their natal web once mature and cease foraging and thus do not replenish their resources (Wise, 1993). In contrast, when males and females are plentiful, lower metabolic rates may come at a cost of decreased capacity for energetically demanding activities such as competitive courtship and rapid mate searching (Shillington, 2005) (but see Mckechnie and Swanson, 2010; Speakman et al., 2004). This suggests a potential trade-off in RMR expression depending on the specific competitive environment an individual encounters.

Here we use male redback spiders to (i) examine whether juvenile males use cues of the availability of females and the density of rivals to alter their metabolic rate to support other plastic developmental shifts, (ii) whether there is a trade-off in allocation towards the metabolic rate and other plastic traits, and (ii) whether changes in resource acquisition (i.e. diet) alter this trade-off. Understanding the factors that are responsible for intraspecific variation in RMR will provide a better understanding of the role of RMR in fitness and as a reflection of quality (Lailvaux and Kasumovic, 2011).

2. Materials and methods

2.1. Spider collection and rearing protocol

Spiders were outbred offspring of individuals collected in Sydney, NSW, Australia. The general rearing protocols can be found in Andrade and Banta (2002) and Kasumovic and Andrade (2006), but we discuss the protocol here briefly. We reared spiders within a common room and kept each egg sac in individual $6 \times 4 \times 4$ cm plastic cages (Amac Plastics, California) where spiderlings were initially reared communally to mimic natural conditions. At the third instar, we removed individuals from communal cages and isolated them in separate $2 \times 2 \times 3$ cm cages. We fed all spiders *Drosophila* sp. twice weekly and monitored all individuals daily to identify males, which are distinguishable from females at the fourth

(penultimate) instar due to the visible development of intromittent organs (Forster and Kingsford, 1983).

We reared penultimate instar males in the presence or absence of virgin females and their webs to mimic extremes of female density in nature and randomly placed these males on one of three diets (high, mid, or low) (according to Kasumovic and Andrade, 2006). We fed high and mid-diet males 2 and 1 *Drosophila* (respectively) 3 times per week, while low diet males received 1 *Drosophila* each week. In the female-present treatment, we surrounded males within a diet treatment by 4 web-building virgin females (each in their own cage). There was no tactile or visual contact between males and females or their webs, but cages were porous to allow the passage of airborne pheromones. Males in the female-absent condition were reared in the absence of females in a separate room due to the difficulty in ensuring complete pheromonal isolation. Cages were placed in identical fume hoods in these two rooms with reduced airflow and temperature controlled at 25 °C. All spiders were held at the same light cycle. Males were randomly assigned to treatments; however we placed more males in the lower diet treatments as we expected higher mortality at low diets.

In both treatments, the number of individually caged neighboring males varied throughout the experiment due to the addition of newly molted penultimate males from the stock population and because males were immediately removed after sexual maturity. Although this resulted in a variable number of males in each treatment at any given time, this mimicked the variation found in natural populations that results from differences in the time of season, population density and due to males maturing, beginning to search for mates, and dying. The number of males in each treatment was a random variable. This was not fixed given that unpredictable variation in development rates in the stock population and the different treatments would make it difficult to collect enough males for a viable experiment to be performed. An alternative would have been creating different male density treatments akin to the diet manipulation, but such a $3 \times 3 \times 2$ design was not possible given the necessity of preventing pheromonal contamination by isolating males in the different rooms. Instead, we calculated the average number of sexually mature males an individual was reared with per day by counting the total number of neighboring males present in the treatment during the male's entire penultimate instar, and dividing by the number of days the focal male took to develop (Kasumovic and Andrade, 2006). This allowed us to use average male density as a covariate and statistically control any variation in our analysis. The average number of males did not differ between treatments ($p > 0.36$).

We monitored males daily and noted the date of sexual maturity. We used development rate (reciprocal of development time) in further analyses. For all males, we measured the length of the patella-tibia of their two front legs at the penultimate instar and the adult stage using digital images and measurement software (Simple PCI, Compix Inc. Imaging systems, 2002) and calculated size at each stage as the average of the two leg measurements. We measured relative male growth by calculating the change in male size controlled for penultimate male size ([5th instar size − 4th instar size]/4th instar size). We also weighed males at maturity (Ohaus explorer balance accurate to 0.01 mg) and calculated male body-condition by using residuals of log (cubed root of male weight) regressed on log (size) (see Kasumovic and Andrade, 2006 for justification of the use of condition residuals).

2.2. Metabolic rate measurements

We used stop flow CO_2 respirometry to estimate RMR of males immediately upon sexually maturity (Lighton, 1991). Web building spiders do not feed shortly prior to and after maturity and complete digestion before molting (Wise, 1993). As males were not

starved, our metabolic measurements were not a measure of basal metabolic rates. However, since males were not fed two days before molting and were monitored during trials to ensure no movement, our results provide reliable and biologically relevant measurement of routine metabolic rates as this is the time period during which males would first leave their webs and begin searching for females.

We took metabolic measures using a Qubit systems (Ontario, Canada) 8 channel gas controller (G245), a Qubit systems 8 channel gas switcher (GS244) and a Li-Cor (Nebraska, USA) CO_2 analyzer (LI-6252) where incoming CO_2 was removed by filtering the air through soda lime. Prior to recording RMR, we took a baseline CO_2 measurement from empty test chambers. Test chambers consisted of cylindrical glass tubes 10 cm in length with a 3 cm diameter and were plugged at both ends with steel plugs and rubber o-rings. All measurements were taken in the dark under red light in a temperature controlled room (at 25 °C) throughout day (between 9:00 and 17:00). Although the chambers were clear to allow us to ensure all males were still, orb-web spiders have poor eyesight such that any visual stimuli would be effectively invisible to males under red light.

Once the control reading was complete, we placed males in the empty chambers and allowed them to settle before taking any measurements (approximately 10 min). We took three consecutive repeated measures of CO_2 production where we watched males and ensured remained motionless during a 4 min period during which air and expired CO_2 was kept within the chamber (=dwell period). Trials where males moved were ignored. At the end of the dwell period, the air (with CO_2 produced by the spider) was flushed from the chamber and flowed through a magnesium perchlorate plug to remove moisture before entering the CO_2 analyzer. The flow rate through the chambers was set to 160 ml/min and did not appear to disturb the spiders.

We subtracted the average baseline CO_2 measurements to yield expired CO_2 estimates for each male and averaged the three readings. We report metabolic rates as CO_2 μmol h^{-1} mg^{-1}. This is appropriate for our sample since the log energetic rate regressed on log body weight is $y = 0.97x - 3.63$ ($n = 108$) (i.e. the mass scaling exponent is not significantly different from 1.0; see Lighton, 1991; Tanaka and Itô, 1982).

2.3. Statistical analysis

We used a GLM with a binomial distribution and a logit link to examine whether survival to maturity was affected by diet and female presence. We next examined whether RMR, size, body-condition and development rate were affected by female presence (factor), diet (factor) and male density (covariate). We initially used a MANCOVA with all second order interactions between factors and covariates to ensure homogeneity in slopes (Engqvist, 2005; Sokal and Rohlf, 1995; Zar, 1984). As all the second order interactions were non-significant, they were removed from the final model (Engqvist, 2005; Sokal and Rohlf, 1995; Zar, 1984). We next used a two-way ANCOVA to create a model with female presence, diet and average male density (covariate) to examine their effects on development. We used Student's t-tests for post-hoc analyses to determine which diets affected each trait. All data were normally distributed and we used SPSS v19 to complete all analyses.

3. Results

Of the 160 males we placed randomly in the six treatments, a total of 108 males successfully reached maturity (Table 1). There was a significant effect of diet on mortality rates with mortality

Table 1
Sample sizes and deaths.

Female presence	Diet		
	High	Mid	Low
Absent	17 (19)	24 (34)	19 (30)
Present	18 (20)	18 (25)	12 (32)

Sample sizes of surviving males in our 2 × 3 rearing design with the total number of males placed in each treatment in brackets.

lowest on the high diet ($\chi^2 = 18.16$, $df = 2,154$, $P < 0.0001$; Table 1). There was no effect of female presence ($\chi^2 = 0.49$, $df = 1,154$, $P = 0.48$) or a female presence × diet interaction ($\chi^2 = 2.38$, $df = 2,154$, $P = 0.30$) on mortality.

Our MANCOVA showed an overall significant effect of female presence ($F_{4,100} = 4.38$, $P < 0.0001$), diet ($F_{8,200} = 16.41$, $P < 0.0001$) and male density (covariate; $F_{4,100} = 3.04$, $P = 0.02$) on the adult phenotype.

Exploration of individual effects with a two-way ANCOVA demonstrated that diet affected all developmental traits with males maturing more quickly and in better body-condition on a higher energy diet (significant Student's; Table 2, Fig. 1). Growth and RMR, however, were only significantly lower in the low diet with no differences between the mid and high diets (significant Student's t test; Table 2, Fig. 1). Female presence significantly affected development rate and growth with males developing faster and maturing smaller in the presence of females (Table 2, Fig. 1). There was a significant positive correlation between male density and RMR and a significant negative correlation between male density and body-condition (Table 2, Fig. 2). There were nearly significant positive effects of male density on growth and development rate ($P = 0.06$ and $P = 0.056$; respectively).

Despite the significant correlations of male density with RMR and body-condition, there was no correlation between RMR and body-condition ($F_{1,106} = 0.61$, $P = 0.43$). The results were the same if weight was substituted for body-condition in this analysis ($F_{1,106} = 0.35$, $P = 0.55$).

4. Discussion

The metabolic rate has evolved in response to abiotic factors such as temperature and diet during development as well as being a function of life-history and phenotypic traits such as development rate and size/weight at maturity (Burton et al., 2011; Chown and Gaston, 1999; Clarke and Fraser, 2004; Gillooly et al., 2001; Munoz-Garcia and Williams, 2005; West et al., 2001). Here we demonstrate that the routine metabolic rate (RMR) is significantly correlated with male density at all diets, just as is the case for other phenotypic traits that are strongly correlated with fitness in this species (Kasumovic and Andrade, 2006). Most importantly, as all the focal males were housed individually, our results eliminate direct intrasexual competition as a potential explanation for this variance, thereby leaving the assessment of pheromones from rivals as the most likely trigger for plastic changes in the metabolic rate.

Nutrient restriction in spiders significantly decreases RMR which is thought to be adaptive as this reduces energy consumption during a period of decreased resource abundance (Bozinovic et al., 2007; Cruz-Neto and Bozinovic, 2004; Steyermark et al., 2005; Stoltz et al., 2010). Along with a decrease in growth rates, poorer body-condition and a longer development time, we show that a decrease in dietary energy also decreased RMR (Fig. 1, Table 2). This is particularly interesting in these sit-and-wait predators for which a low RMR would decrease energy consumption and may allow prolonged survivorship, especially when food resources

Table 2
ANCOVA results.

	Routine metabolic rate		Development rate		Growth		Body-condition	
	F (df)	P	F (df)	P	F (df)	P	F (df)	P
Female presence	0.20 (1, 103)	0.65	7.89 (1, 103)	**0.006**	10.12 (1, 103)	**0.002**	0.52 (1, 103)	0.47
Diet	3.02 (2, 103)	**0.05**	35.82 (2, 103)	**<0.0001**	7.00 (2, 103)	**0.001**	20.26.(2, 103)	**<0.0001**
Male density	5.26 (1, 103)	**0.02**	3.00 (1, 103)	0.09	3.16 (1, 103)	0.08	6.03 (1, 103)	**0.02**

Results from an ANCOVA examining the effects of female presence, diet and male density on the routine metabolic rate, development rate, growth and body-condition of male spiders. Significant results are in bold.
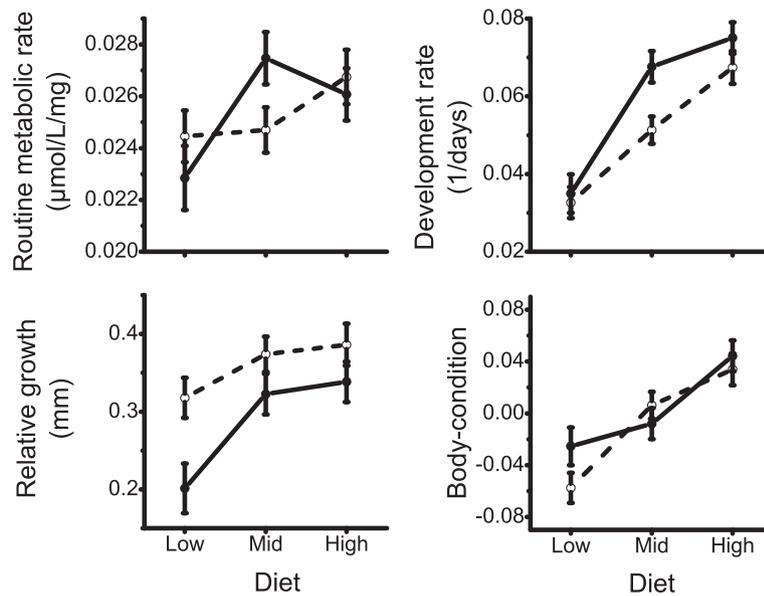
Fig. 1. The effect of diet and female presence (filled circles) and absence (empty circles) on the routine metabolic rate, development rate, growth and body-condition (residuals of cubed root of weight regressed on size) of developing redback males.
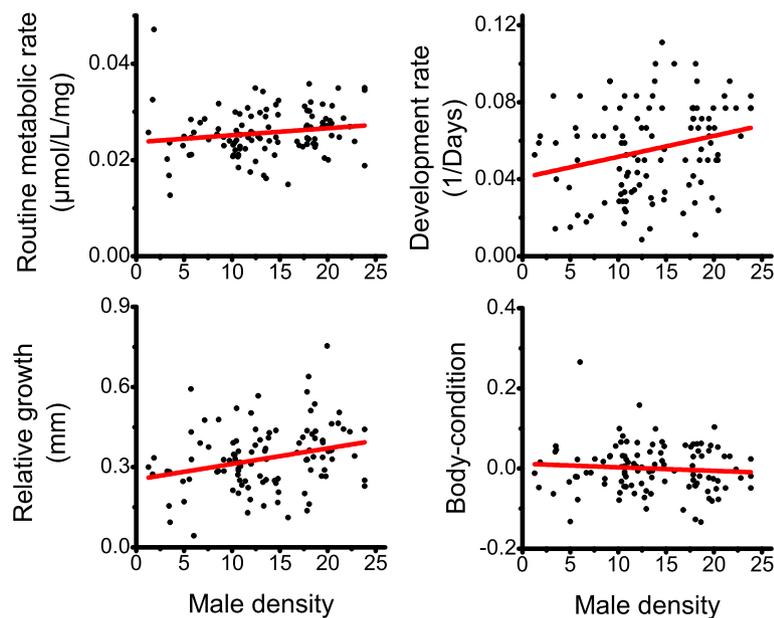
Fig. 2. The effect of male density on the routine metabolic rate (r^2 adj = 0.01), development rate (r^2 adj = 0.06), growth (r^2 adj = 0.06) and body-condition (residuals of cubed root of weight regressed on size; r^2 adj = −0.002) of developing redback males of males across all treatments. Figures are based on the full model (r^2 = 0.16).

are limited (e.g., our low-diet treatment) (Stoltz et al., 2010). Most importantly, as male redbacks do not feed once they begin mate searching, a reduction in RMR may be adaptive as it would allow males to conserve their limited energy reserves. Consistent with this idea, RMR was lower for low-diet males than other diet treatments (Fig. 1).

Our results replicate previously demonstrated allocation shifts towards growth, body-condition and development rate in male redback spiders (Kasumovic and Andrade, 2006), and expand the implications of these effects by demonstrating that RMR changes with the social environment. Most notably, RMR was positively correlated with male density while there was no correlation with weight or body-condition. Moreover, RMR of adult males increased as the number of potential rivals increased regardless of whether or not females were present (Table 2, Fig. 1) even with the observed increase in development rate with female presence. This suggests that several different cues are used by males to make developmental decisions and that resource allocations towards various phenotypic traits are, at least to some extent, independent of one another. Despite the significant positive correlation between male density and RMR, our model suggests male density only explains 1% of the variation in RMR. The role of male density in the expression of RMR may nevertheless be biologically relevant however, as factors known to affect RMR in other taxa (Burton et al., 2011; Chown and Gaston, 1999), such as development rate, weight, and diet, each explained less than 10% of the variation in RMR in this study (i.e. 6%, 6% and 9% of the variation, respectively).

Increased stress during development is known to affect metabolic rates during maturity (Criscuolo et al., 2008; Holliday et al., 2009; but see Krause et al., 2009). Although our diet results can support either a stress hypothesis as the lower energy in our study resulted in lower metabolic rates as in other studies (Criscuolo et al., 2008; Holliday et al., 2009), the correlation between RMR and male density is not consistent with a stress effect. Males in our study increased their metabolic rates when reared in greater densities rather than reducing them as in other studies (DeLong and Hanson, 2009; Deng et al., 2008). Increased RMR is argued to be positively related to maximal attainable metabolic rates in invertebrates (see Reinhold, 1999; Shillington, 2005) which fuels increased locomotor activity in spiders (Johnston et al., 2007; Kotiaho et al., 1998; Shillington, 2005; Tanaka and Itô, 1982; Watson and Lighton, 1994) (but see Mckechnie and Swanson, 2010; Speakman et al., 2004 for arguements for and against in endotherms). This is likely particularly important in redback males as high activity levels are required to succeed against rivals in scramble competition (Kasumovic and Andrade, 2009; Snow and Andrade, 2004, 2005) and competitive courtship against rivals (Stoltz and Andrade, 2010). Although we currently do not know the role that RMR plays in direct competition in male redbacks or how they compare to maximal rates, our results agree with studies demonstrating that subordinate males increase their RMR when the likelihood of competition increases (Millidine et al., 2009; Senar et al., 2000). Further studies examining male competition under various diet treatments are necessary to elucidate whether our observed RMR shifts are adaptive.

Interestingly, our RMR values are approximately 2.5 times higher (mean ± SD; 0.6239 ± 0.0001 $\mu l\,h^{-1}\,mg^{-1}$) than other published results on other spider species (0.25–0.270 $\mu l\,h^{-1}\,mg^{-1}$) (Jensen et al., 2010; Kotiaho et al., 1998; Schmitz, 2004; Tanaka and Itô, 1982). Differences in life-history and morphology may explain these different rates of energy expenditure (Wise, 1993) as we examined a web-building species, whereas these other studies focused on wandering spiders. Further studies on the metabolic rates of web building species are required to determine the degree of variation in spiders and the mechanistic causes of these differences.

5. Conclusion

Many studies demonstrate that adult interactions with conspecifics can affect metabolic rates (Millidine et al., 2009; Schluter et al., 2007; Senar et al., 2000; Sloman et al., 2000). Currently, we have a limited understanding of how earlier juvenile social environments affect the adult RMR. Here we demonstrate that cues available while males are immature also result in changes in the metabolic rate to match the competitive challenges they will encounter at adulthood. Understanding large scale patterns in RMR may thus require consideration of other ecological and life-history variables such as the type of mating system, mating opportunities and intensity of competition rather than exclusively focusing on factors such as diet, temperature and phylogeny (e.g., Burton et al., 2011; Chown and Gaston, 1999; Clarke and Fraser, 2004; Munoz-Garcia and Williams, 2005). Further studies examining how internal physiological processes vary as a consequence of competitive environments and whether they support metric and life-history traits will provide insight into the evolution of RMR and provide a more holistic understanding of male quality in general (Houle, 2011; Lailvaux and Kasumovic, 2011).

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