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# Metabolic efficiency in courtship favors males with intermediate mass in the Australian redback spider, *Latrodectus hasselti*



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## ABSTRACT

Recent studies have suggested that metabolic efficiency may be an important factor in male mating success when females require vigorous and/or prolonged courtship. In capital breeding animals in which a male's resource pool is fixed at adulthood the relationship between energy expenditure and courtship performance may be especially important, as males are expected to utilize their finite resources efficiently when soliciting mates. Males may benefit from being efficient, i.e., achieving a sufficiently high level of courtship signaling at low energetic cost, if it enables them to acquire mates before their limited energy reserves are depleted. We investigated the relationship between metabolic efficiency and courtship vibrational signaling in the Australian redback spider, *Latrodectus hasselti*, a semelparous capital breeder where males invest heavily in courtship to secure a mating. We assessed metabolic rate in a sample of males and measured two courtship components (duty cycle and amplitude) that reflected the energy content of web-borne vibrations. We then calculated two indices of metabolic efficiency for these courtship properties. There was a quadratic relationship between mass and duty cycle such that the highest duty cycle signals were performed by males having intermediate mass. Furthermore, intermediate-mass males were also the most metabolically efficient. Prolonged courtship is necessary in *L. hasselti* for successful mating, and the results of this study suggest that intermediate-mass males are superior courtiers because they utilize their finite resource pool most efficiently to produce high energy vibrational signals.

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## 1. Introduction

Courtship is an essential precursor to mating for many species (Andersson, 1994). A substantial body of evidence shows that high courtship activity is often associated with increased mating success largely because females are more likely to mate after a vigorous courtship (Carranza and Trucios, 1993; Cook et al., 2013; De Luca and Cocroft, 2008; Knapp and Kovach, 1991; Kotiaho, 2002; Parker, 1974; Stapley, 2008). Much research has focused on examining physiological traits that influence courtship activity, to better understand links between male performance and female choice. One trait that has been the focus of some recent research is the active metabolic rate (AMR), which reflects the amount of energy a male expends while soliciting mates (Gillooly and Ophir, 2010; Kasumovic and Seebacher, 2013; Reinhold, 1999; Stoddard and Salazar, 2011). Generally, high AMR is positively correlated with the level of courtship activity

because displays that are louder, longer, or both, require more energy to produce, and females tend to prefer males that display at these higher levels (Bailey et al., 1993; Halliday, 1987; Kotiaho et al., 1998; Prestwich, 1994; Reinhold et al., 1998; Wells and Taigen, 1989). Related to AMR is metabolic efficiency, which measures energy expenditure per unit of courtship activity (Bailey et al., 1993; Watson and Lighton, 1994). In a recent review, Hill (2011) suggested that the most metabolically efficient males (i.e., those achieving a sufficiently high level of courtship signaling at low energetic cost), are likely to represent superior courtiers because such males demonstrate a capacity to optimize energy expenditure between advertisement and somatic maintenance (Stoddard and Salazar, 2011; Thomson et al., 2014; Watson and Lighton, 1994; Watt, 1986). Uncovering how factors such as AMR, metabolic efficiency, and courtship performance interact can be challenging, though, because male energetic rates during courtship may fluctuate over a male's reproductive lifetime due to changes in body condition or energy reserves (Sadd et al., 2000; White et al., 2013), reproductive status (Clutton-Brock, 1984; Clutton-Brock and Albon, 1979), or social conditions (Candolin, 2000; Stoltz et al., 2012).

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Some of these complexities may be simplified in taxa where males have a fixed resource pool at adulthood that is not replenished (capital breeders, Stearns, 1992), and limits on the availability of females predicts maximal performance with no trade-offs for future mating opportunities (e.g., monogyny, Fromhage et al., 2005). In such systems, because males will usually encounter only one female in their lifetime (Andrade, 2003), all their energy reserves should be expended, if necessary, to secure a mating. At the same time, however, a finite resource pool necessitates efficient allocation of energy reserves throughout the mate acquisition process (i.e., searching, courtship, and mating) in order to ensure that resources are not depleted before a male has performed sufficient courtship to be accepted by the female (Hill, 2011). Accordingly, this predicts a positive relationship between energy reserves and metabolic efficiency for males most likely to be successful at obtaining a mate. For example, in the Sierra dome spider, *Linyphia litigiosa*, body mass is positively correlated with two complementary measures of courtship metabolic efficiency, and large mass, high efficiency males are successful in aggressive encounters with other males and at siring more offspring (Watson and Lighton, 1994).

Here, we examine links between metabolic rate, male phenotype, and courtship performance in monogynous, capital-breeding male redback spiders (*Latrodectus hasselti*). Upon reaching sexual maturity, male *L. hasselti* abandon their webs in search of females. During this time they cease foraging and must rely on energy reserves accumulated during development, which severely limits their energetic budget and contributes to a mate-search mortality rate exceeding 80% (Andrade, 2003). Field-caught adult males vary considerably in size and mass (Andrade, 2003), as do males reared in the laboratory under uniform conditions and fed the same diet (Stoltz et al., 2008), which suggests that inherent differences among males in their ability to accumulate and use energy reserves may be an important factor influencing variability in mate searching success. When a female is found, a male will not abandon her in search of another (Andrade, 2003; Andrade and Kasumovic, 2005), and males that succeed in mating are eaten by the female and so will not have another opportunity to mate (Forster, 1992). Male fitness therefore depends entirely on a single mating event, and thus males are expected to expend their total energy reserve towards securing that sole reproductive opportunity. However, following mate-searching males must engage in a lengthy courtship display that involves producing web-borne vibrational signals for a minimum of 100 min to secure a mating (Stoltz and Andrade, 2010). Even if males mate successfully, courtship duration determines the female's likelihood of remating with another male (Stoltz et al., 2009). This is perhaps why courtship in this species often includes up to 5 h of vibrational signaling and movement on the female's web (Forster, 1995). Vibrational signaling is expected to be an energetically demanding form of communication (Kotiaho et al., 1998; Lighton, 1987; Randall, 2014), and the extended courtship of male *L. hasselti* suggests performance may be limited by energetic expenditure. Consistent with this, a continuous 3-h bout of courtship significantly decreases male longevity, and males initially in poor condition suffer the highest longevity cost (Kasumovic et al., 2009).

While duration is indeed an important courtship trait in this species, the role of signal energy is less well understood, yet we expect it to also comprise an important courtship feature in this species. High energy signals are expected to be more attractive to females because they provide more stimulation to her sensory system (Morris et al., 1978; Stoddard and Salazar, 2011), and that is likely to be critical here. *Latrodectus* females' webs vary considerably in size, with some that are very large relative to the size of the spiders (Szlep, 1965; M. Andrade, personal communication). A mate searching male entering a female's web is unlikely to know

her exact position and therefore would be expected produce high energy signals in order to elicit and maintain her attention until she can be found (Bailey et al., 1990; Brenowitz, 1986; Maklakov et al., 2003). This is not a foregone conclusion though, as a recent study of a congener suggested that males may produce low energy 'whispers' during the initial phase of courtship to distinguish them from struggling prey (Vibert et al., 2014). Clearly, more data is needed to adequately assess the role of signal energy on courtship performance in *Latrodectus* spiders.

In this study, we investigate the relationships between metabolic rate, male phenotype and courtship vibrational signaling in *L. hasselti* using stop-flow gas respirometry and laser Doppler vibrometry. We first examine the metabolic expenditure of males during courtship compared to resting to determine if courtship vibrational signaling is energetically demanding. We then quantify courtship activity by measuring two components of web-borne vibrations related to the energy content of signals: (1) duty cycle (proportion of time spent producing vibrational signals during a courtship bout), and (2) amplitude (intensity or 'loudness' of courtship vibrations). We then use these properties to calculate a male's metabolic efficiency (amount of energy expended per unit of courtship activity). Finally, we assess potential associations between metabolic efficiency and two aspects of male phenotype (body size and mass) to test the hypothesis that in *L. hasselti* larger males represent superior courtiers because they are most metabolically efficient at producing high energy vibrational signals.

## 2. Materials and methods

### 2.1. Spider rearing and maintenance

We used spiders that were derived from an outbred laboratory-reared population established with individuals collected in the field from New South Wales, Australia in 2007, and replenished with additional wild-caught spiders in 2009. Spiderlings were held with siblings in clear plastic cages (9 × 9 × 11 cm, Amac Plastics) in a temperature-controlled room at the University of Toronto Scarborough at 25 °C on a 12:12 light:dark cycle. We removed spiderlings at the 4th instar to ensure they remained virgins (males become sexually mature at the 5th instar and females around the 7–8th) and kept them individually in plastic containers (9 × 9 × 11 cm). We fed spiderlings with flies (*Drosophila melanogaster*) twice a week, and fed adult females immature house crickets (*Acheta domesticus*) once per week.

### 2.2. Metabolic rate measurements

We used expired CO<sub>2</sub> as a measure of metabolic rate (Stoltz et al., 2012). For each male in our experiment, we measured metabolic rates during rest and during courtship in two separate sessions performed on the same day. We conducted experiments in a laboratory at the University of Toronto Scarborough from January to March, 2010. All measurements were taken in a temperature controlled room (25 °C) under red light during the central 8 h of a 12 h scotophase. We took metabolic measures using stop-flow gas respirometry with a Qubit systems (Kingston, Ontario, Canada) 8 channel gas controller (G245), a Qubit systems 8 channel gas switcher (GS244) and a Li-Cor (Nebraska, USA) CO<sub>2</sub> analyzer (LI-6252) where incoming CO<sub>2</sub> was removed by filtering the air through soda lime. The test chamber consisted of a cylindrical glass tube (12 × 2.5 cm) sealed at both ends with steel plugs and rubber o-rings. Briefly, for each trial, air was flushed into the chamber and kept there for a sampling period that lasted either 70 s (courtship) or 3 min (resting). At the end of each sampling period the air was flushed from the chamber and flowed through a magnesium

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