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Temporal patterns of nutrition dependence in secondary sexual traits and their varying impacts on male mating success

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Variation in the quantity of nutrients ingested over an individual's lifetime is likely to differentially affect distinct male secondary sexual traits and courtship signals, potentially providing females with information about a male's past and present foraging history. We hypothesize that female choice is thus influenced by a male's lifetime foraging history. To test this, we manipulated the quantity of nutrients (i.e. prey items) available to male wolf spiders, *Schizocosa stridulans*, using a fully crossed 2 × 2 design with low versus high prey quantity across juvenile and adult life stages, and assessed the impact of these diet treatments on male foreleg pigmentation, courtship rate and mating success. We found foreleg pigmentation to be dependent upon both juvenile and adult diet, with increased nutrition dependence of pigmented versus unpigmented leg segments. Despite this, the degree of foreleg pigmentation did not predict mating success. In contrast, courtship rate was not nutrient dependent, yet strongly predicted mating success. Finally, we found a significant interaction between juvenile diet, adult diet and courtship rate on mating success. Males that experienced a diet switch (low juvenile to high adult, LH; high juvenile to low adult, HL) exhibited no relationship between courtship rate and mating success, while those that experienced a consistent diet (LL; HH) showed increased mating success with increased courtship rates. Our results suggest that nutrition dependence of secondary sexual traits is not necessarily a predictor of their role in mating success and that female mate choice is the result of complex interactions between multiple male traits.

Within a single season, individuals may experience rapid shifts in food availability. For males, especially those with multicomponent (or multimodal) mating displays, this variability may have serious implications on future mating success. Not only can components of a male's courtship display vary in their sensitivity to changes in food intake, but the timescales over which these components respond can also be variable. Because of this, multicomponent courtship displays have the potential to convey information concerning the nutritional history of an individual over a variety of timescales. Understanding how such fluctuations are reflected in male secondary sexual traits and how these traits, in turn, influence mating success is therefore of significant interest for sexual selection and communication research.

Shifts in food availability can occur for many reasons. For example, the density of small arthropods, a common prey type for numerous predators, is affected by rainfall (Shultz, Lensing, & Wise, 2006; Staley et al., 2007) and temperature (Bale et al., 2002; Pearce-Higgins, Dennis, Whittingham, & Yalden, 2010), both of which may change unexpectedly. Additionally, for ectothermic predators, rate (and potentially efficiency) of foraging is positively correlated with temperature (Kruse, Toft, & Sunderland, 2008). Therefore, short-term temperature fluctuations may affect foraging success even if they do not directly affect prey density. Evidence supports the notion that the frequency of extreme environmental or climatic fluctuations, as well as the degree of variability in seasonal weather, is increasing (Coumou & Rahmstorf, 2012; Easterling et al., 2000; Schär et al., 2004; Yeh et al., 2009), suggesting that the likelihood that populations will experience unexpected or stochastic fluctuations in prey availability may also be on the rise, further emphasizing our need to understand the effect of variability in food availability on sexual signalling systems.

Fluctuations in diet can have various effects on male mating displays, depending on when and if display components are diet sensitive. On the one hand, morphological traits are often mostly impacted by juvenile diet. Many characters become fixed after production (e.g. avian plumage) or after maturation, but nutrition intake prior to maturation can affect the resources available to

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produce pigmentation or ornamentation (Ohlsson, Smith, Raberg, & Hasselquist, 2002; Taylor, Clark, & McGraw, 2011; Uetz, Papke, & Kilinc, 2002). On the other hand, energetically demanding behaviours such as elaborate courtship displays may be more strongly affected by adult (or current) diet, which has an impact on available energetic resources (Brown, 2011; Droney, 1996, 1998; Dussourd, Harvis, Meiwald, & Eisner, 1991; Kolluru & Grether, 2004; Wedell, 1994). However, these trends in dietary life-history effects on behavioural and morphological traits are far from universal. Juvenile diet may affect adult behaviour by having an impact on neurological development (Nowicki, Hasselquist, Bensch, & Peters, 2000; e.g. the developmental stress hypothesis, reviewed in Spencer & MacDougall-Shackleton, 2011) or by influencing the development of morphological traits associated with the production of the behavioural display (e.g. Scheuber, Jacot, & Brinkhof, 2003). Similarly, morphological traits such as ornaments can be affected by current diet if they require maintenance such as preening or cleaning (e.g. Griggio, Hoi, & Pilastro, 2010), or if they contain vascularized tissue (e.g. goldfinch bill colour, Rosenthal, Murphy, Darling, & Tarvin, 2012; booby foot colour, Torres & Velando, 2003). Traits that reflect a male's dietary life history can provide discriminating females with information about his quality as a mate. In fact, female preferences for honest displays may lead to the evolution of signal components that are more sensitive to changes in condition (i.e. heightened condition dependence; see Grafen, 1990; Iwasa & Pomiankowski, 1994; Pomiankowski, 1987). In complex courtship displays that encompass multiple distinct components (e.g. morphological traits and dynamic movement displays), one might predict different display components to be influenced by foraging rates at different life stages, thus revealing different patterns of condition dependence, potentially providing females with information about the lifetime foraging history of a male.

We test the hypothesis that distinct components of the complex courtship display of *Schizocosa stridulans* wolf spiders demonstrate different temporal patterns of nutrient dependence and that variable nutrient intake across life stages will influence a male's reproductive success. *Schizocosa* wolf spiders provide an excellent system for examining temporal patterns of nutrient-dependent secondary sexual traits and their impact on male mating success, as males exhibit a wide range of multicomponent and multimodal courtship behaviours (reviewed in Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013). Complex courtship displays often comprise pigmented legs that are waved or tapped to produce dynamic visual displays. The foreleg pigmentation is absent prior to a male's maturation and, in some species, is influenced by juvenile diet (*Schizocosa ocreata*: Hebets, Wesson, & Shamble, 2008; Uetz et al., 2002; *Schizocosa uetzi*: Shamble, Wilgers, Swoboda, & Hebets, 2009; *Schizocosa floridana*: Rosenthal & Hebets, 2012). In addition to foreleg pigmentation, males also produce a substrate-transmitted acoustic 'song', which is usually both necessary and sufficient to elicit copulations (for review, see Hebets et al., 2013; but see Stafstrom & Hebets, 2013). Female mate choice behaviour in wolf spiders is as complex as the male's display. For example, in *Rabidosa rabida,* female mating decisions may be age or condition dependent (Wilgers & Hebets, 2012), and in both *Rabidosa* and *Schizocosa* species, the visual and vibratory components of the male's display can interact to affect the likelihood of copulation (Hebets, Stafstrom, Rodriguez, & Wilgers, 2011; Stafstrom & Hebets, 2013; Wilgers & Hebets, 2012). Components of complex display can also vary in their temporal patterns of nutrition dependence, which can ultimately influence male mating success. Prior research using *S. floridana* demonstrated that male foreleg darkness was influenced by juvenile diet whereas adult body condition (measured as body mass/carapace width) was influenced by adult diet (Rosenthal & Hebets, 2012). Interestingly, in this species, diet was found to interact with courtship rate to affect copulation success; courtship rate was a strong predictor of copulation success for all males except those that switched from a high-quantity diet before maturation to a low-quantity diet after maturation (HL), suggesting that variability experienced by a male may have an impact on females' assessment of his display.

Here, we build on previous studies by examining the potential temporal patterns of nutrition dependence in secondary sexual traits (pigmentation and courtship rate) and body condition in the conspicuously dimorphic wolf spider *S. stridulans*, a forest floor predator found in the southeastern United States. Mature males possess dark pigmentation on the first pair of walking legs (forelegs), which covers both the tibia and patella and can extend as far as halfway up the femur (Stratton, 1991). The foreleg tibiae also have short brushes of black hair (Stratton, 2005), further enhancing the visual contrast between the pigmented and unpigmented leg segments. During courtship, males tap their first pair of legs repeatedly and vigorously in front of the female (Stratton, 1991). This display is accompanied by a 'song' consisting of the vibrations produced by the leg taps, as well as vibratory components produced through abdominal tremulation and palpal stridulation (Elias, Lee, Hebets, & Mason, 2006). As in many other *Schizocosa* species, courtship rate (measured as leg taps/min) is a strong predictor of copulation success in *S. stridulans* (Hebets et al., 2011), and it is likely that leg taps correlate with bouts of vibratory signalling. Despite the presence of conspicuous pigmentation, however, previous studies suggest that it is the vibratory component that is necessary and sufficient to elicit copulations (Hebets, 2008; Hebets et al., 2011). Nevertheless, foreleg pigmentation has been found to have an impact on female assessment of male courtship; increased pigmentation is suggested to reduce the strength of female preference for higher courtship rates, allowing more pigmented males to gain copulations at lower rates (Hebets et al., 2011). Given the putative interaction between courtship rate and foreleg pigmentation in *S. stridulans*, we sought to explore the potential temporal pattern of nutrition dependence in these traits and their role in male mating success.

We used a 2×2 full factorial design of low versus high nutrient/food availability during juvenile and adult life stages in male *S. stridulans* to (1) assess the temporal patterns of nutrition dependence in two male secondary sexual traits (foreleg pigmentation and courtship rate) as well as body condition, (2) determine which components of the male's display predict mating success, and (3) explore the potential interactions of diet and courtship rate on male mating success. Based upon prior research in this and other *Schizocosa* species, we predicted that the degree of tibial pigmentation would be strongly affected by juvenile diet, that courtship rate would be unaffected by diet and that body condition would be influenced by adult diet or the interaction between juvenile and adult diet. We further predicted that tibial pigmentation acts as an indicator trait, and that it would be more sensitive to diet than overall body pigmentation. In terms of mating success, we predicted condition-dependent mating success. Additionally, given the previous evidence for the possibility of an interaction between diet and courtship rate (Rosenthal & Hebets, 2012), we predicted that courtship rate would be the strongest predictor of copulation success in all males except those experiencing a high juvenile/low adult food treatment.

METHODS

Spiders and Diet Manipulation

Subadult *S. stridulans* (~4 weeks pre-maturation; $N = 1431$) were collected at night on 3–5 April 2011 in Lafayette County, MS,