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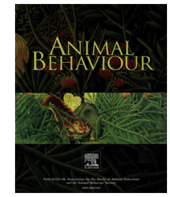

Influence of dietary nutrient balance on aggression and signalling in male field crickets

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Indicator models of sexual selection predict that sexually selected trait elaboration should covary positively with condition. However, nutrition might influence the expression of multiple traits, where high-quality diets may result in positive trait correlations and low-quality diets in trade-offs. Although previous studies have examined how diet quantity or single nutrients, such as protein, carbohydrate and phosphorus, influence sexual traits, few have examined how dietary nutrient balance affects sexual trait expression. We therefore investigated how dietary protein:carbohydrate ratio and percentage of phosphorus influence the relationship between investment in mate attraction signalling and aggression. We fought groups of six adult male *Gryllus veletis* crickets, each consuming a unique diet, while recording their prefight and postfight signalling parameters. We found no evidence that diet influenced aggression or prefight signalling, with the exception that high-phosphorus diets had a negative influence on several signalling effort parameters. Body size was an important predictor of aggressive behaviour and most signalling parameters, suggesting that developmental diet may have a greater influence on these sexual traits. Several prefight signalling parameters were weakly related to aggression, suggesting that signalling may advertise competitive abilities. Males consuming high-carbohydrate and equal protein:carbohydrate diets experienced changes in signalling parameters that represented an overall increase in signalling effort following aggressive contests compared to males consuming high-protein diets, suggesting that dietary effects on signalling may only become apparent following periods of highly energetic activity. Changes in signalling following aggressive contests were also related to aggression levels modulated by dietary phosphorus content, such that only males consuming low-phosphorus diets were able to invest heavily in signalling after investing heavily in aggression. Our findings highlight the importance of research on the interplay between multiple sexually selected traits, and how dietary nutrient balance influences these relationships.

Sexual selection is a major driving force in the evolution of elaborate male secondary sexual traits (Andersson, 1994; Darwin, 1871). Indicator models of sexual selection predict that the expression of elaborate male traits involved in mate attraction and male–male competition should covary positively with individual condition (Grafen, 1990; Kodric-Brown & Brown, 1984; Maynard Smith, 1985; Pomiankowski, 1987; Zahavi, 1975, 1977). Furthermore, when males possess multiple elaborate sexually selected traits (e.g. field crickets: Alexander, 1961; guppies: Kodric-Brown & Nicoletto, 2001; birds: McGraw, Mackillop, Dale, & Hauber, 2002), they can be correlated if their production depends on similar aspects of condition, or uncorrelated if they reflect different aspects of condition or the same aspect over different timescales (Candolin, 2003; Johnstone, 1996; Møller & Pomiankowski, 1993). Thus, male sexual traits are expected to serve as honest indicators of condition to potential mates and rival male competitors (Berglund, Bisazza, & Pilastro, 1996; Johnstone, 1995; Lailvaux & Irschick, 2006; Maynard Smith & Harper, 2003).

Nutrition is an important source of variability in an individual's somatic state, which in combination with epigenetic and genetic components, make up the primary determinants of individual condition (Hill, 2011). The nutrients acquired by an organism may collectively constitute a pool of resources that are allocated to various physiological processes that support somatic maintenance, growth, development, reproduction and elaborate sexually selected trait expression (Hill, 2011; Rowe & Houle, 1996; Tomkins, Radwan, Kotiaho, & Tregenza, 2004). There is abundant evidence that mate attraction signalling is influenced by diet (reviewed by Cotton,

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Fowler, & Pomiankowski, 2004b; Johnstone, 1995), but much of this research has focussed on simplistic measures of nutrition, such as overall diet quantity or the importance of single nutrients (Cotton et al., 2004b; Hill, 2011). For example, consuming greater amounts of food or more nutrient-dense food is often associated with increased ornamentation or sexual signalling (e.g. stalk-eyed flies: Cotton, Fowler, & Pomiankowski, 2004a; crickets: Holzer, Jacot, & Brinkhof, 2003; Whattam & Bertram, 2011; wolf spiders: Kotiaho, 2000; cowbirds: McGraw et al., 2002). Similarly, individual nutrients such as protein (crickets: Hunt et al., 2004; fruit flies: Yuval, Kaspi, Shloush, & Warburg, 1998) and phosphorus (crickets: Bertram, Schade, & Elser, 2006; Bertram, Whattam, Visanuvimol, Bennett, & Lauzon, 2009) also influence sexual signalling. Unfortunately, dietary manipulation of total food quantity or the amount of a single nutrient does not take into account the nutritional complexity of natural foods.

The balance of multiple dietary nutrients is an important component of an individual's resource pool, as the functioning of vital physiological processes and the expression of different phenotypic traits may depend on different optimal ratios of nutrients ('intake target', sensu Raubenheimer & Simpson, 1993). Dietary nutrient ratio could therefore potentially influence relationships between multiple male sexual traits if, for example, their expression depends on differing optimal nutrient ratios, or if a priority allocation of a limiting nutrient towards one trait negatively affects the expression of another (Rowe & Houle, 1996; Tomkins et al., 2004). Additionally, both surpluses and deficits of nutrients from eating imbalanced foods can result in fitness costs, including reduced reproductive output, obesity, malnutrition or toxicity (Huggins, Navara, Mendonça, & Hill, 2010; Raubenheimer & Simpson, 2006; Raubenheimer, Lee, & Simpson, 2005). Thus, researchers are shifting towards nutritionally explicit approaches to understand the influence of diet on mate attraction signalling and other sexual traits (e.g. amphipods: Goos, Cothran, & Jeyasingh, 2016; crickets: Harrison, Raubenheimer, Simpson, Godin, & Bertram, 2014; Maklakov et al., 2008; flies: Sentinella, Crean, & Bonduriansky, 2013; cockroaches: South, House, Moore, Simpson, & Hunt, 2011).

Comparatively fewer studies have examined the influence of nutrition on aggressive behaviours related to male–male competition, with most studies using crude measures of individual energy reserves, such as body weight or weight corrected for size (e.g. Bertram & Rook, 2012; Brown, Smith, Moskalik, & Gabriel, 2006; Fitzsimmons & Bertram, 2012; Wilson et al., 2010). Only two studies to date have used a nutritionally explicit approach that considers how dietary nutrient ratio influences aggression or dominance (crickets: Han & Dingemanse, 2017; cockroaches: South et al., 2011). Collectively, these studies have provided mixed support for an influence of nutrition on aggressive behaviour in the context intrasexual competition. However, in nonsexual contexts, dietary composition and overall hunger levels have been found to influence aggression (e.g. crickets: Adamo & Hoy, 1995; birds: Andersson & Åhlund, 1991; spiders: Andrade, 1998; ants: Grover, Kay, Monson, Marsh, & Holway, 2007). Clearly, further research is needed on the extent to which dietary nutrient balance influences aggression in the context of male–male competition.

In field crickets (Grillidae), both acoustic mate attraction signalling and male–male aggression influence male reproductive success (Alexander, 1961). Male field crickets compete in aggressive (agonistic) contests with rivals for access to mating territories, from which they signal acoustically to attract mates from a distance (Alexander, 1961). Female field crickets prefer to mate with males that produce higher-effort acoustic mate attraction signals (Hirtenlehner & Römer, 2014; Holzer et al., 2003; Scheuber, Jacot, & Brinkhof, 2004; Wagner, 1996) and males that are successful at winning fights (Nelson & Nolen, 1997; Savage, Hunt, Jennions, & Brooks, 2005). While field crickets are frequently used as model organisms in studies of animal aggression (e.g. Adamo & Hoy, 1995; Bertram, Rook, Fitzsimmons, & Fitzsimmons, 2011; Judge & Bonanno, 2008) and acoustic signalling (e.g. Harrison et al., 2014; Maklakov et al., 2008), little research has been done on examining relationships between these sexually selected behaviours. There is evidence that higher aggression levels are related to more 'proactive' behavioural profiles that include greater motility, exploration and general activity (e.g. Rose, Cullen, Simpson, & Stevenson, 2017), leading to the expectation that aggression may be related to signalling activity. There is some evidence that aggression might be related to fine-scale temporal (e.g. pulse and chirp rates), amplitude and frequency aspects of cricket acoustic signals (Bertram & Rook, 2012; Brown et al., 2006). However, previous studies examining correlations between aggression and broad-scale measures of mate attraction signalling effort in field crickets have found no relationship (e.g. total signalling time, signalling bout duration, signalling bout rate: Fitzsimmons & Bertram, 2012; Wilson et al., 2010). Thus, how these two components of male field cricket reproductive success are related to one another remains unclear.

Both acoustic signalling and aggression are energetically costly behaviours for male crickets, resulting in a two-fold to 13-fold increase in oxygen consumption over resting rates (Hack, 1997; Hoback & Wagner, 1997; Prestwich, 1994). Additionally, agonistic contests between rivals typically involve a stereotypical escalating sequence of discrete behaviours (Adamo & Hoy, 1995; Alexander, 1961), with energetic expenditure increasing with both contest duration and level of escalation (Hack, 1997). Carbohydrate metabolism appears to be the main source of energy for fuelling increased metabolic activity in muscle tissue associated with acoustic signalling (Thomson, Darveau, & Bertram, 2014) and agonistic contests (Briffa, 2008), and increasing the ratio of dietary carbohydrate relative to protein content appears to be positively correlated with acoustic signalling effort in crickets (Maklakov et al., 2008). Acoustic signalling effort in crickets is also positively associated with increased phosphorus intake (Bertram et al., 2009), which may be due to phosphorus (an important component of RNA) fuelling the repair and replacement of damaged proteins in muscles and other tissue involved in high metabolic activity (Bertram et al., 2006). Only one study to date has examined the influence of dietary nutrient balance of protein, carbohydrate and phosphorus on acoustic mate attraction signalling in any species (crickets: Harrison et al., 2014). To our knowledge, the combined influence of these nutrients on other metabolically costly traits, such as aggressive behaviour, has not been examined.

In the current study, we investigated how dietary protein, carbohydrate and phosphorus composition influence investment in acoustic mate attraction signalling and aggressive behaviour in male spring field crickets, *Gryllus veletis*. Our aim was to answer the following three questions. (1) How does dietary nutrient composition influence signalling and aggression? (2) How is signalling related to aggression, and does dietary nutrient composition influence the relationship? (3) Do males alter their signalling behaviour following agonistic contests, and are these changes related to their level of aggression or dietary nutrient composition? We predicted that individuals consuming diets high in carbohydrates (i.e. low protein:carbohydrate ratio) and phosphorus would invest more heavily in both signalling and aggression, whereas individuals consuming diets low in both carbohydrates and phosphorus would be unable to afford the costs of both high-effort signalling and aggression, resulting in either reduced investment in both behaviours or a trade-off between them. Similarly, we predicted that when males invest heavily in aggression, only males