



# When do acoustic cues matter? Perceived competition and reproductive plasticity over lifespan in a bushcricket



Darren Rebar<sup>\*</sup>, Michael D. Greenfield

Institut de Recherche sur la Biologie de l'Insecte (IRBI), UMR 7261, Faculté de Sciences et Techniques, Tours, France

## ARTICLE INFO

### Article history:

Received 15 September 2016

Initial acceptance 1 November 2016

Final acceptance 6 February 2017

MS. number: 16-00815R

### Keywords:

experience-mediated plasticity  
nuptial gifts  
postcopulatory sexual selection  
social environment  
sperm competition  
terminal investment

Individuals often modify their behaviour in response to environmental cues and their own condition. Here we asked whether males modify ejaculates based on information from the sociosexual environment and their physiological age, and how those two factors may interact. We used two populations of the chorusing bushcricket, *Ephippiger diurnus*, to test whether males strategically adjust large, costly spermatophores they transfer to females during mating based on experience of rivals' calls, and whether males change their investment strategies with age. Males broadcast highly consistent, rhythmically repeated calls of syllables in daily choruses. Populations differ in average syllable number, an important trait under selection via female preference, and females from our two populations prefer calls with more syllables than the population mean. We reared males in one of five acoustic environments that varied in call syllable number. We then mated males twice, as young and old adults, measuring spermatophore size each time. We found that acoustic experience, age and their interaction all significantly influenced male investment, resulting in reaction norms with different slopes. Young males differentially invested in spermatophores in response to acoustic experience, whereas old males generally invested in larger spermatophores across environments. We then tested for a broad pattern of age-related investment with eight different field-collected populations, finding the majority of old males significantly increased spermatophore investment. Our findings demonstrate that both environmental context and an individual's life history state influence plasticity in reproductive investment, and such adjustments may optimize their reproductive success.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals may adjust their reproductive investment in response to their condition, such as physiological age, as well as to both abiotic and biotic environmental factors (Cornwallis & Uller, 2010; Cotton, Small, & Pomiankowski, 2006; Miller & Svensson, 2014; Qvarnström, 2001). Some environmental factors, such as the sociosexual environment, are variable, and individuals are often behaviourally plastic to such cues because of their profound effect on reproductive fitness (Andersson, 1994; Kokko, Jennions, & Brooks, 2006; West-Eberhard, 1983, 2014). For example, hearing male advertisement signals influences a neighbouring male's behaviour (e.g. Kasumovic, Hall, Try, & Brooks, 2011; Rebar & Rodríguez, 2016) and also the behaviour of local females (Hebets & Sullivan-Beckers, 2010; Rodríguez, Rebar, & Fowler-Finn, 2013; Verzijden et al., 2012). In response to physiological age and social experience, individuals are thus predicted to trade off reproductive

investment across mating events when mating is costly, favouring increased investment when the benefit is high or the likelihood of a future mating event is low (Roff, 1992; Stearns, 1992; Wedell, Gage, & Parker, 2002).

In males, adjustment of ejaculate investment (e.g. spermatophores in insects) to various cues is expected. For example, males may increase investment with increasing physiological age (Clutton-Brock, 1984; Williams, 1966). Life history theory predicts that reproductive effort should reflect an individual's condition or their remaining longevity (i.e. physiological age), a notion supported by work on various aspects of chronological versus physiological age (e.g. Levine, 2013; Ligout, Munier, Marquereau, & Greenfield, 2012). Males may also modify their investment based on the social environment. These adjustments may be mediated by experience, such as the presence or absence of rival male calls during development, or to the immediate presence of rivals during mating (Bretman, Gage, & Chapman, 2011; Kasumovic & Brooks, 2011; Kelly & Jennions, 2011). Such adjustments occur in response to sperm competition, and sperm competition models offer straightforward predictions on how males will adjust

<sup>\*</sup> Correspondence and present address: D. Rebar, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

E-mail address: [dr451@cam.ac.uk](mailto:dr451@cam.ac.uk) (D. Rebar).

ejaculate investment to the probability that two ejaculates compete, termed 'risk', and to the number of different males' ejaculates competing for a female's eggs, termed 'intensity'. In general, males will increase ejaculate investment when a rival is present, but decrease it with additional rivals due to increased sperm competition intensity (Engqvist & Reinhold, 2005; Parker, 1998; Parker, Ball, Stockley, & Gage, 1997; Parker & Pizzari, 2010).

Many mating behaviours, such as male signals and female mate preferences, remain flexible through adulthood (e.g. Rebar, Barbosa, & Greenfield, 2016; Rodríguez, Boughman, et al., 2013; Swanger & Zuk, 2015), and male ejaculate expenditure should similarly fluctuate in response to physiological age and the risk and intensity of sperm competition. The question remains, though, whether and how these factors interact with one another over an individual's life. Does one have priority over the other? Or is each factor more important in regulating investment at different times? Selection should favour investment by males that optimize their lifetime fitness across mating events.

In species in which males use advertisement signals to attract mates, males can use rivals' signals to assess the social environment, and ultimately sperm competition. Numerous male behaviours are sensitive to acoustic cues, including male ejaculate expenditure to sperm competition risk (Bretman, Gage, et al., 2011; Bretman, Westmancoat, Gage, & Chapman, 2011; Gray & Simmons, 2013; Kasumovic & Brooks, 2011; Kasumovic et al., 2011). Studies on ejaculate investment have predominantly centred on the presence or absence of cues, but the range of adjustments males could make to acoustic cues is much broader. For instance, males could adjust ejaculate investment based on the quality of perceived rivals, as is the case for precopulatory behaviours to rival cues (Kasumovic et al., 2011; Lane et al., 2015; Yoshikawa, Ohkubo, Karino, & Hasegawa, 2016). Or males could adjust ejaculate investment based on how females adjust their behaviour, such as mate preference or remating rate, to acoustic cues. Male adjustments to female adjustments have been documented in signalling behaviours (Bertram, Harrison, Thomson, & Fitzsimmons, 2013; Kahn, Dolstra, Jennions, & Backwell, 2013). For example, male fiddler crabs adjust their courtship effort to match the shift in female mate preferences across a mating period (Kahn et al., 2013). Acoustic signals can thus provide information about the quantity and quality of rivals and about how females will adjust their mating behaviour. Males may thus be selected to respond to what these cues say about likely sperm competition risk and intensity.

Here we used a long-lived, multiply mating chorusing insect, the flightless bushcricket, *Ephippiger diurnus* (Orthoptera: Tettigoniidae) (Hockham, Graves, & Ritchie, 2004), to test how male age and acoustic experience may interact to influence the size of male spermatophores. Males were tested shortly after attaining reproductive maturity and approximately 10 days later, an age interval that is expected to affect their physiological condition. Acoustic experience refers to long-term exposure to acoustic treatments to which individuals were subjected in the laboratory from late juveniles through adulthood, except at the moment of mating. The species is distributed in geographically isolated populations that tend to be genetically, morphologically and behaviourally differentiated (Party, Streiff, Marin-Cudraz, & Greenfield, 2015; Spooner & Ritchie, 2006). Males call in daily choruses for up to 6 h per day to attract mates (Duijm, 1990; Ritchie, 1991, 1992). Each call is composed of syllables, and the average number of syllables is population specific (Ritchie, 1992). There is some variation between individuals in each population, but syllable number within individuals is highly repeatable (Barbosa, Rebar, & Greenfield, 2016b; Rebar et al., 2016). Females consistently favour calls with more syllables than the population mean in our two study populations (Barbosa, Rebar, & Greenfield, 2016a), even with call experience

(Rebar et al., 2016). Upon mating, males produce large nuptial gifts, spermatophores composed of a sperm-filled ampulla and nutritional spermatophylax that are up to 40% of their body weight (Busnel & Dumortier, 1954; Wedell, 1994a). This investment is costly, as evidenced by an average postmating refractory period of 4 days before males can mate again (Vahed, 2007; Wedell, 1993). Whether spermatophore and ejaculate investment reflects parental investment (i.e. nutrition) or mating investment (i.e. sperm protection or increased female refractory period) remains unknown for many bushcricket species (Lehmann, 2012; see Quinn & Sakaluk, 1986 for a general introduction to the alternative functions). For instance, nuptial gift consumption by females in another bushcricket species decreased then increased feeding over the short term (24 h), but not over the long term (4.5 days; Lehmann & Lehmann, 2016). In other words, nutritional gifts such as spermatophores can be complex, and determining their specific consequences to females can be challenging. Nevertheless, both hypotheses predict that larger spermatophores would result in delayed female remating and thus yield increased fitness returns for the male. Therefore, repeatable male songs, known female preferences and large spermatophores make *Ephippiger* an ideal species for investigating whether condition and environment influence a male's investment, and if so, how these two influences interact.

Previously, we experimentally manipulated male experience of rivals' calls from late juveniles through adulthood by rearing males in one of five acoustic environments that varied in call syllable number. We found that young *Ephippiger* males adjusted spermatophores in response to the acoustic environment, but that this response was not simple (see Rebar et al., 2016). Young males increased spermatophore size when exposed to some song compared to no song, but decreased spermatophore size as the song stimuli became more attractive or varied.

Here we extended on that previous work in several ways. First, we continued to investigate the complex relationship between male investment and acoustic environments. The previous data came from one population and in 1 year; the relationship needed to be confirmed to rule out the possibility of a spurious effect. We note that the inverted U-shaped relationship observed in the preliminary experiment (Rebar et al., 2016) matches predictions from sperm competition risk and intensity. We thus undertook the current study to obtain sufficient data to address these predictions across populations and years. Second, we tested whether males modified spermatophores as they aged. We used population level reaction norms (Foster, 2013) as a graphical device to highlight the changes in the slopes of the mean phenotypes expressed in each environment across mating events, noting that this does not necessarily imply any genotype-specific effects. Third, we addressed the interplay between age and perceived sperm competition by comparing investment patterns across acoustic environments as males age.

We predicted that young males would adjust spermatophore size in a manner consistent with sperm competition risk and intensity, increasing spermatophore size when some calls were present due to increased sperm competition risk (e.g. Bretman, Gage, et al., 2011; Gray & Simmons, 2013). However, we predicted that males would decrease spermatophore size as call attractiveness increased. Previous work on female preference for male syllable number evaluated in single-stimulus tests shows that females walk longer distances towards a high-syllable number song than towards a song composed of fewer syllables (Barbosa et al., 2016a; Rebar et al., 2016). The distance travelled in these single-stimulus tests reflects a female's attraction towards a particular call type and her 'motivation' to mate with a male broadcasting that song. In the field, females would arrive in the vicinity of such males more often than those producing less attractive songs. We inferred that

متن کامل مقاله

دریافت فوری ←

**ISI**Articles

مرجع مقالات تخصصی ایران

- ✓ امکان دانلود نسخه تمام متن مقالات انگلیسی
- ✓ امکان دانلود نسخه ترجمه شده مقالات
- ✓ پذیرش سفارش ترجمه تخصصی
- ✓ امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
- ✓ امکان دانلود رایگان ۲ صفحه اول هر مقاله
- ✓ امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
- ✓ دانلود فوری مقاله پس از پرداخت آنلاین
- ✓ پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات