



What makes a good mate? Factors influencing male and female reproductive success in a polyphagous moth



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The mating propensity of an individual is expected to depend on the costs and benefits of mating, which may vary across the sexes and across different mating opportunities. Both males and females should gain fitness either by mating with multiple mates and/or by mating with higher quality mates. Therefore, an important question in the area of sexual selection concerns what makes an optimal mate. From a female perspective, females are expected to prefer males providing direct material benefits for the present generation and/or indirect genetic benefits for their offspring in the subsequent generation. Because the male's contribution to these benefits can be limited, as reproduction imposes nontrivial costs on males, the female's benefits from mating can vary markedly as a function of the condition of her mate. In capital breeding species, in which males invest most of their larval resources in a single reproductive event, the females are likely to prefer to mate with virgin males in good condition (i.e. males that have developed on high-quality food sources). In this study we used the European grapevine moth, *Lobesia botrana*, to test experimentally whether the larval nutrition and mating history of males influence their quality as mates. We provided wild *L. botrana* males originating from different cultivars and vineyards with unlimited access to standardized females, and examined the lifetime reproductive success of the males and the consequences for the reproductive output of females. Our results show that 'male quality' depended on both the male larval origin and mating history, and that females discriminated between males and mated more with males having high spermatophore quality (virgin males and males from certain cultivars or vineyards) to obtain substantial direct benefits.

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The mating propensity of an individual is expected to depend on the costs and benefits of mating, which may vary across the sexes and the number of mating opportunities. When both male and female vary in their reproductive quality, the two sexes are expected to be choosy and should display higher mating preferences with partners providing higher fitness benefits. Males and females should gain fitness either by mating with multiple mates (Arnqvist & Nilsson, 2000; Wagner, 2011) and/or by mating with higher quality mates. Therefore, an important question in the sexual selection area concerns what makes an optimal mate for the choosy sex. 'Mate reproductive quality' is determined by a variety of behavioural, physiological and morphological traits (Lailvaux & Kasumovic, 2010; Wilson & Nussey, 2010). These traits influence the propensity to mate of individuals (through precopulatory

behaviours including courtship, production of sex pheromone and mate guarding) and therefore influence their probability of being chosen as a mate and shape their realized fitness (Simmons, 2001).

The benefits of mate choice depend on the quality of the chosen mate but also on the extrinsic and intrinsic conditions of the choosy individual, including its physiological state and physical and social environment. For example, some studies have shown that males mate preferentially with more fecund females (Bonduriansky, 2001) and tailor their ejaculate size to the level of sperm competition (Wedell, Gage, & Parker, 2002). In the same way, female mating behaviour is affected by a variety of intrinsic (including mating status or age) and extrinsic factors (such as predation risk, parasite infection or mate availability). Because females that fail to mate have zero fitness (Rhainds, 2010), the level of female choosiness is constrained by the risk of remaining unmated, which depends on demographic effects, low mate encounter rate, out-competition by rivals or prereproductive death (Kokko & Mappes, 2005; Rhainds, 2010, 2013). Thus, female mating strategies often reflect a trade-off between maximizing the benefits of obtaining

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high-quality mates, reducing the probability of mating failure and minimizing other mating costs (Rhainds, 2010). Keeping in mind these trade-offs, good mates for females are those that are able to provide direct and indirect benefits (Møller & Jennions, 2001). Indirect benefits can arise from genetic traits of the chosen male (e.g. good genes), which lead to increased fitness of the resulting offspring (Mays & Hill, 2004; Tregenza & Wedell, 2000). Direct benefits are related to whether the chosen male is sufficiently fertile, free of disease, or able to provide parental care, access to territories or to nutritive resources including nuptial gifts (Choe & Crespi, 1997; Vahed, 1998). However, the male contribution to these direct benefits can be limited, as reproduction imposes nontrivial costs on males, arising from mate location, competition, courtship, parental care and especially ejaculate production (Janowitz & Fischer, 2010; Paukku & Kotiaho, 2005; Scharf, Peter, & Martin, 2013). Thus, female benefits from mating can be extremely variable based on the quality of their mate, because factors limiting the reproduction of males can have profound consequences for female reproductive output.

For species in which males provide females with material resources including a nutritive ejaculate (for example, spermatophores in some lepidopteran species), the influence of male mating frequency on future reproductive output can also be extremely pronounced (Torres-Vila & Jennions, 2005; Wedell et al. 2002). Because ejaculate production is costly (Dewsbury, 1982), male performance usually declines across multiple matings, leading to diminishing reproductive returns for males (reviewed by Simmons, 2001). Moreover, males may be limited in the amount of sperm they can transfer to a female during mating (Marcotte, Delisle, & McNeil, 2005), and male mating history (the number of previous matings) is certainly a key factor determining female fitness, especially in species in which males can keep copulating despite being sperm depleted (Damiens & Boivin, 2006; Steiner, Henrich, & Ruther, 2008). It has been commonly assumed that males have to face trade-offs between investment in somatic maintenance and investment in reproduction because they have finite resources to invest (Barnes & Partridge, 2003; Stearns, 1992). Such trade-offs typically arise under food limitation, because male expenditure in ejaculate production is constrained in part by resource availability; consequently, males have to invest in either current or future reproduction (Simmons, 2001). In capital breeders, which rely mainly on larval reserves for successful reproduction, the resources needed to produce a nutritive ejaculate can be a limiting factor. Therefore, ejaculate production could be related to the number of copulations and male larval nutrition, but few studies have reported the quantitative and qualitative relationships involved. Diet quality can have a significant influence on the rate at which males produce ejaculate, the quality of the seminal fluid proteins and the effectiveness of the ejaculate in achieving fertilization (Arnqvist & Danielsson, 1999; Gage & Cook, 1994; Simmons & Kvarnemo, 1997). When males lack adequate protein sources or when they have developed on nutritionally limited host plants, critical depletion of their ejaculate generally occurs during successive matings (Gage & Cook, 1994). However, most studies have focused on the factors affecting male reproductive output following emergence, particularly during the first two mating events (Cordes et al. 2015; Delisle & Hardy, 1997; Tigreros, 2013) but not on the trade-off between larval nutrition and the male's entire lifetime reproductive investment.

In this context, our study goals were to assess whether (1) larval nutrition is important for male mating capacity and lifetime reproductive investment, (2) male larval nutrition and male mating history together affect males' quality as mates and (3) females prefer to mate with 'high-quality mates' in order to obtain larger direct benefits. To answer these questions, we used the European

grapevine moth, *Lobesia botrana* (Lepidoptera: Tortricidae), which is a very important pest of grapes worldwide. Several studies of this species have already shown marked effects of larval nutrition on male and female fitness (Moreau, Benrey, & Thiéry, 2006; Moreau, Thiéry, Troussard, & Benrey, 2007; Muller, Thiéry, Moret, & Moreau, 2015). However, the lifetime reproductive capacity of male moths of this species remains unknown because most studies have concerned only the first mating of individuals (Moreau et al. 2006, 2007; Muller et al. 2015; see Torres-Vila, Rodríguez-Molina, Roehrich, & Stockel, 1999 for an exception). In the present study, we provided wild *L. botrana* males that developed on different grape cultivars and in different vineyards with unlimited access to females and investigated the lifetime reproductive success of the males. We also investigated the consequences for the reproductive output of females as a function of male larval origin and mating history. In a first step we explored variation in male reproductive investment (spermatophore size, number of sperm) during successive matings. We predicted that (1) male reproductive investment and mating capacity would be affected by male larval nutrition on different cultivars and (2) male quality would depend on both their larval nutrition and mating history. In a second step, we studied the consequences of male larval nutrition and mating history on the reproductive output of females (fecundity and fertility). We predicted (3) that female fitness would be affected by both male larval origin and mating history and (4) that females would be more motivated to mate with males of 'high quality', thus receiving larger nutrient-rich spermatophores.

METHODS

Field Sampling

Lobesia botrana is a major pest of grapes. It is widely distributed in most European vineyards and is now present in the U.S.A., where three or four larval generations occur each year, depending on latitude. First-generation larvae of *L. botrana* were collected in the field during June 2013. To test for a cultivar effect within a given population, larvae were sampled from three grape, *Vitis vinifera*, cultivars ('Carignan', 'Mourvèdre' and 'Grenache') in the same vineyard (Perpignan, France; 42°44'7.063"N, 2°52'56.441"E), ensuring the same abiotic conditions (temperature, light exposure, humidity) for larval development. The three chosen grape varieties are biochemically very different, especially in their phenolic contents (Teissedre & Chervin, 2011). Indeed, 'Carignan' and 'Grenache' grape extracts contain less total phenols than Mourvèdre grape extracts (Jensen, Demiray, Egebo, & Meyer, 2008). To test for a geographical effect, we sampled larvae from the cultivar 'Grenache' from two additional geographically distinct French vineyards: Estézargues (43°56'49.781"N, 4°39'39.372"E) and Sénas (43°43'54.251"N, 5°1'45.621"E). Larvae were sampled at the end of the larval cycle (fifth instar), following construction of glomerulae made of flower buds aggregated in larval silk (phenology 17–25; Eichhorn & Lorenz, 1977). Larvae usually complete their development in a single grape bunch, and each glomerulus is only occupied by a single larva (Torres-Vila, Stockel, & Rodríguez-Molina, 1997). To collect newly emerged adults, larvae at the end of their development were placed in large polyethylene boxes (60 × 40 cm and 21 cm high) in the laboratory and fed ad libitum on grape bunches from the same cultivar and site where they developed, and were incubated at 22 ± 1 °C, 60 ± 10% relative humidity, and under natural photoperiod conditions. The larvae were checked daily until pupation at which time they were gently removed from their glomerulae. The pupae were weighed to the nearest 0.1 mg using a Precisa 262 SMA-FR microbalance, placed individually in glass tubes (70 × 9 mm diameter) stoppered with cotton wool plugs, and

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