



Old male mating advantage results from sexual conflict in a butterfly

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Accumulating evidence suggests that sexual conflict is all pervasive, although cooperation is evidently needed in sexually reproducing organisms. While male mating success is typically positively associated with resource-holding potential, old male mating success prevails in some organisms despite old males being in greatly reduced condition. We tested whether this counterintuitive pattern is the outcome of (1) sexual conflict or (2) female preference for older males in the tropical butterfly *Bicyclus anynana*. Our results support the first hypothesis as females that mated with older compared to younger males showed reduced hatching success of eggs and higher remating propensity, and tended to show shorter refractory periods. Thus, females apparently try to compensate for reduced fitness arising from mating with older (low-quality) males by being more willing to remate, especially with young and/or virgin (high-quality) males. As mating with older males negatively affects female fitness, old males may acquire a mating advantage by being more aggressive and persistent during courtship, in line with the residual reproductive value hypothesis. Thus, males increase their own reproductive success at the expense of their female partners, such that the ‘cooperation–conflict balance’ between the sexes seems to be shifted towards conflict in *B. anynana*.

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In sexually reproducing organisms, cooperation between males and females is evidently necessary to produce offspring. However, accumulating evidence suggests that sexual conflict occurs very frequently, challenging the traditional view of sexual interactions being harmonious events. Sexual conflict is defined here as the differences in the evolutionary interests between males and females (Chapman et al. 2003). It ultimately arises because reproduction typically induces nontrivial costs in both males and females, including ejaculate and offspring production and parental care (Enquist & Leimar 1990; Chapman et al. 1998; Kemp & Wiklund 2001; Pauku & Kotiaho 2005). Consequently, differential selection pressures on males and females result in individuals trying to maximize their own genetic reward, regardless of the potential fitness consequences for the sexual partner (Arnqvist & Rowe 2005; Bergmann et al. 2011). For males, for instance, sexual selection is expected to favour traits increasing the number of matings and sperm competitive ability, even if such adaptations may have detrimental effects on female partners in terms of reduced fecundity or life span (e.g. Rice 1996, 1998; Arnqvist & Rowe 2005; Wigby & Chapman 2005; Fischer 2007). On the other hand, females will mate with males in a way that maximizes their individual fitness, for instance by using cryptic mate choice

(Eberhard 1996; Schneider & Lesmono 2009). Consequently, the males’ reproductive investment may not result in successful fertilization of eggs, if their sperm is eventually rejected by the female.

Male mating success in animals is typically positively related to proxies indicating resource-holding potential such as body mass or fat content (Marden & Waage 1990; Kemp & Wiklund 2001). Consequently, male mating success often increases with age in vertebrates, presumably because of enhanced resource-holding potential (i.e. an increase in mass) and enhanced experience (Kemp 2006). In contrast to vertebrates though, in many invertebrates, and especially in holometabolous insects, physiological condition (body mass, fat content) clearly diminishes with age (Karlsson 1994; Kemp 2002; Fischer et al. 2008). Note that holometabolous insects no longer grow after adult eclosion, but draw heavily on resources accumulated during the larval phase (Bauerfeind & Fischer 2005b; Boggs & Freeman 2005). Additionally, spermatophore size (Kaitala & Wiklund 1995; Cook & Wedell 1996; Marcotte et al. 2005; but see e.g. Wedell & Ritchie 2004), sperm number and possibly also sperm quality (Wedell & Ritchie 2004; Damiens & Boivin 2006) are expected to decrease with age. Against this background it is interesting to note that old male mating advantage has been demonstrated in several insect species including beetles, crickets, fruit flies, butterflies and moths (e.g. Zuk 1988; Conner 1989; Simmons & Zuk 1992; Cameron et al. 2005; Fischer et al. 2008; Perez-Staplez et al. 2010; Nieberding et al. 2012). This pattern is counterintuitive, as, in insects, mating with

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an older male may actually decrease female fitness (Kotiaho & Simmons 2003; Martin & Hosken 2004; Pauku & Kotiaho 2005). Therefore, female insects are expected to mate preferentially with younger rather than older males (Wedell & Karlsson 2003; Ferkau & Fischer 2006; Fricke & Maklakow 2007). As expected, mating with younger males has been found to be advantageous in, for example, the mosquito *Anopheles gambiae* (Chambers & Klowden 2001), the European corn borer, *Ostrinia nubilalis* (Milonas & Andow 2010), and the ladybird *Coccinella septempunctata* (Srivastava & Omkar 2004), while in other systems no effects of male age could be observed (Fricke & Maklakow 2007; Perez-Staplez et al. 2010).

Old male mating advantage may, in principle, result from either (1) increased competitive ability/eagerness to mate in older than younger males, (2) females preferring older over younger males or (3) a combination of both. An increased eagerness to mate in older males (e.g. more persistent and aggressive courtship behaviour) is predicted by the residual reproductive value hypothesis, owing to diminishing chances of future reproduction (Williams 1966; Kemp 2002, 2006; Fischer et al. 2008). Younger males, in contrast, will generally pay greater costs to their future reproductive potential from being killed or injured during mating or courtship (Parker 1974; Enquist & Leimar 1990). Consistent with the residual reproductive value hypothesis, old male mating advantage has been found to be associated with greater eagerness and aggressiveness of older males (*Hypolimnas bolina*: Kemp 2002; *Bicyclus anynana*: Geister & Fischer 2007; Fischer et al. 2008; Janowitz & Fischer 2010). Given that females are expected to mate preferentially with younger rather than older males (see above), old male mating advantage enforced by male aggressiveness may indicate sexual conflict. On the other hand, female preference for older males could be based on either the latter's proven high fitness in terms of survival, thus essentially reflecting a 'good genes' hypothesis (Trivers 1972; Brooks & Kemp 2001; Mays & Hill 2004), or on older males transferring more sperm and/or accessory gland products to the females upon mating, which may directly increase their reproductive success (e.g. Oberhauser 1997; Wiklund et al. 1998; Wedell & Karlsson 2003).

In the tropical butterfly *B. anynana* older males have a substantially higher mating success than younger males (Fischer et al. 2008; Janowitz & Fischer 2010; Nieberding et al. 2012), although physiological condition is known to diminish with age (evidenced by a decrease in body mass and fat content and an increase in wing wear with increasing age, Fischer et al. 2008). The ultimate and proximate reasons underlying this striking pattern though are under debate (Fischer et al. 2008; Nieberding et al. 2008, 2012).

On the one hand, increased old male aggressiveness based on a low residual reproductive value has been suggested to cause old male mating advantage (Fischer et al. 2008; cf. Fischer 2006; Geister & Fischer 2007), while, on the other hand, females may mate preferentially with older males based on their proven survival ability, facilitated by age-specific changes in sex pheromone profiles (Nieberding et al. 2008, 2012). By investigating female reproductive output, remating propensity and refractory period we set out to test whether old male mating advantage in *B. anynana* is likely to result from sexual conflict (male aggressiveness; 'sexual conflict hypothesis') or cooperation (female choice; 'female preference for older males hypothesis'). Predictions associated with the 'sexual conflict hypothesis' are that females that have mated with an older compared to a younger male should show (1) reduced reproductive output, (2) a shorter refractory period and (3) higher remating propensity. While prediction (1) rests on the assumption of diminishing condition with age (see above), predictions (2) and (3) are based on the expectation that females that have mated with an old (= low-quality) male will mate sooner and more readily for a second time than females that have mated with a young (= high-

quality) male (e.g. Wedell 1991; Kaitala & Wiklund 1995; Hughes et al. 2000). If mating multiply, females may be able to replenish depleted or unviable sperm supplies (e.g. Arnqvist 1989; Siva-Jothy 2000), to gain additional nuptial gifts and nutrients (e.g. Wedell 1997; Wiklund et al. 1998, 2001; Wedell & Karlsson 2003), or to bias paternity towards preferred males (Birkhead & Pizzari 2002; Barbosa 2009; Schneider & Lesmono 2009). Predictions associated with the 'female preference for older males hypothesis' are opposite to those given above, namely that females that have mated with an older compared to a younger male should show (1) increased (or at least not decreased, in the case of indirect fitness benefits) reproductive output, (2) a longer refractory period and (3) lower remating propensity.

METHODS

Study Organism and Rearing Conditions

Bicyclus anynana is a tropical, fruit-feeding butterfly, distributed from southern Africa to Ethiopia (Larsen 1991). This species exhibits striking phenotypic plasticity (two seasonal morphs) as an adaptation to alternate wet–dry seasonal environments and the associated changes in resting background and predation (Lyytinen et al. 2004). In 1988, a laboratory stock population was established at Leiden University, the Netherlands, from over 80 gravid females collected at a single locality in Malawi. Several hundred adults are reared in each generation, maintaining high levels of heterozygosity at neutral loci (Van't Hof et al. 2005). From the Leiden stock population, a laboratory population was established at Greifswald University, Germany, in 2007. From more than 200 females of the latter population eggs were collected for the experiments detailed below. Two cohorts of about 1000 eggs each, with the second cohort being collected 10 days later than the first, were used to produce two age classes of young (2 days) and old (12 days) males that were available simultaneously. Owing to a rapid decrease in daily egg production and a rather short overall adult life span, a difference in life span of 10 days is considered to be ecologically highly relevant in this species (Brakefield & Reitsma 1991; Fischer & Fiedler 2001; Fischer et al. 2008).

Larvae were reared until pupation on young maize plants in a climate chamber at a constant temperature of 27 °C, high relative humidity (70%) and a 12:12 h light:dark cycle, that is, under climatic conditions similar to those at which the butterflies develop and reproduce during the favourable wet season in the field (Brakefield & Reitsma 1991; Brakefield 1997). Pupae were collected daily and kept in cylindrical hanging cages (30 × 39 cm) until adult eclosion. To avoid matings prior to experiments, males and females were separated on their eclosion day. Note that male *B. anynana* are not able to mate immediately after eclosion, such that a separation before eclosion is not necessary. Males are able to mate from day 1 after eclosion onwards. For adult feeding, butterflies were supplied with moist banana and water throughout.

Experimental Design

Two experiments were carried out (for details see below) to analyse whether females gain a fitness benefit from mating with older as compared to younger males, and if females adjust their refractory period and mating propensity when mating with males of different age classes.

Experiment 1: female reproductive output

To determine effects of male age on female reproductive output, 2-day-old virgin females were mated to 2-day-old or 12-day-old virgin males. Therefore, an uncontrolled number of females and

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