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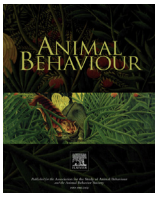

Linking mating preferences to sexually selected traits and offspring viability: good versus complementary genes hypotheses

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Indirect fitness benefits hypotheses suggest that offspring of preferred mates should exhibit greater survival or reproductive success. For example, good genes hypotheses propose that female mating preferences are mediated by secondary sexual traits because they honestly reflect the ability to pass on genes that will enhance offspring survival or reproduction. Conversely, complementary genes hypotheses propose that mating preferences are mediated by complementary genes because they enhance offspring viability. While these two research traditions are not strict alternatives and both may operate simultaneously, they have never been tested together. Here we explore the multiple potential underlying factors influencing mating preference evolution in Jamaican field crickets, *Gryllus assimilis*. After evaluating female preferences for randomly selected males, we tested whether preferred males differed from nonpreferred males in their body size, relative mass or mate attraction signals. We then mated females to their preferred or nonpreferred partners and tested offspring viability. Results revealed: (1) females preferred larger males, (2) larger females oviposited more eggs, (3) neither morphology nor mate attraction signalling explained variation in offspring viability, and (4) mating with a preferred partner did not enhance offspring viability. Overall, in our current study population, cricket mate preferences were inconsistent with complementary genes and good genes hypotheses for indirect fitness benefits. Our current research explores whether male secondary sexual traits honestly reflect the ability to pass on genes that enhance offspring reproduction.

Search for a mate can be costly as it exposes individuals to predators and takes time away from other tasks (Andersson, 1994; Hedrick & Dill, 1993; Houle & Kondrashov, 2002; Hubbell & Johnson, 1987; Hutchinson & Halupka, 2004; Johnstone, 1997; Pomiankowski, 1988; Wiegmann, Angeloni, & Seubert, 2013). Why then have mate preferences evolved? Direct fitness benefits, such as females receiving greater material contributions that enhance their fertility or fecundity, provide easy explanations for the evolution of mate preferences (reviewed by Andersson, 1994; Hamilton, 1990; Hoelzer, 1989; Wagner, 2011). Mate preference evolution may also be explained by indirect fitness benefits such as enhanced offspring viability, parasite resistance of offspring, or the attractiveness of sons in the subsequent generation (Andersson, 1994; Fisher, 1930; Heywood, 1989; Zahavi, 1975). For example, Fisher (1930) and later Zahavi (1975) posited that secondary sexual traits reflect their bearers' health and viability (good genes). When both secondary sexual traits and female preferences are heritable, females that mate with more elaborate males (males with brighter, louder or more complex secondary sexual traits) will produce offspring that may inherit their father's good genes for health and viability, and their mother's good genes for preference, resulting in greater survival and/or reproductive success. A correlation may result between preference and viability (demonstrated by Lande, 1981). The difficulty with these hypotheses is that continuous directional selection for elaborate traits may remove heritable variation, resulting in the elimination of the indirect benefits associated with mate preference (e.g. Andersson, 1994; Borgia, 1979; Falconer & Mackay, 1996; but see Heywood, 1989; Pomiankowski, 1988).

The main rationale for Hamilton and Zuk's (1982) insightful paper on mate choice was to provide a way around the conundrum

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of erosion of variation. Hamilton and Zuk (1982) reasoned that, by associating with males with more elaborate traits, females would avoid exposure to pathogens and parasites and, assuming that appropriate heritable variation exists, their offspring would exhibit greater health and viability. Because pathogens and parasites have much shorter generation times, they evolve rapidly relative to their hosts. Given the evolutionary Red Queen dynamics between hosts and pathogens/parasites, the cycles of coadaptation should ensure a continual source of genetic variation in elaborate traits, provided that elaborate traits are associated with genes for disease resistance.

There is substantial support for Hamilton and Zuk's (1982) hypothesis as males with more elaborate traits are healthier and carry fewer pathogens and parasites than males with less elaborate traits (Balenger & Zuk, 2014; Buchanan, Catchpole, Lewis, & Lodge, 1999; Figuerola et al., 1999; Hamilton & Poulin, 1997; McGraw & Hill, 2000; Merila, Sheldon, & Lindström, 1999; Zuk, 1992), and females often avoid exposure to pathogens and parasites when they associate with males with more elaborate traits (because these males are healthier), thus decreasing the risks to their own health and survival (Balenger & Zuk, 2014; Borgia & Collis, 1989; Lawniczak et al., 2007; McGraw & Hill, 2000; Petrie, Halliday, & Sanders, 1991; Pruett-Jones, Pruett-Jones, & Jones, 1990; Roberts, Buchanan, & Evans, 2004; Sheldon & Verhulst, 1996; Zuk, 1992; Zuk, Johnson, Thornhill, & Ligon, 1990). However, few studies show consistency with Hamilton and Zuk's prediction that more elaborate sexual traits predict offspring health and viability (reviewed in Barber, Arnott, Braithwaite, Andrew, & Huntingford, 2001; Clayton, 1991; Siva-Jothy & Skarstein, 1998). Given weak support for Hamilton and Zuk's offspring viability prediction, more consideration might be given to other indirect fitness benefits hypotheses.

Several indirect fitness benefits hypotheses do not require mating preferences to be proximately dependent on elaborate male sexual traits. Instead, these ‘complementary genes’ hypotheses assume that mating preferences are mediated by heterozygosity or complementary (i.e. dissimilar) alleles (Bluhm & Gowaty, 2004a,b; Brown, 1997; Downhower, Brown, Pederson, & Staples, 1983; Gowaty, 2008, 2010; Gowaty et al., 2007; Penn & Potts, 1999; Wedekind, 1999; Wedekind & Furi, 1997; Wedekind, Seebeck, Bettens, & Paepke, 1995). Individuals should benefit from mating with genetically dissimilar partners because their offspring should have a greater number of heterozygous loci and a reduced probability of expressing deleterious recessive alleles (Tregenza & Wedell, 2000). For example, the immune gene complementarity hypothesis stems from the fact that offspring are often more viable, vigorous, etc., when their parent's immunity genes are complementary (Bluhm & Gowaty, 2004a,b; Gowaty, 2008, 2010; Gowaty et al., 2007). The immune gene complementarity hypothesis echoes the long-standing logic of ‘heterozygote vigour’, where alleles at immunity-related loci act as a defence against pathogens and parasites, and individuals with the highest likelihood of survival often carry the greatest heterozygosity (Colegrave, Kotiaho, & Tomkins, 2002; Kempenaers, 2007; Neff & Pitcher, 2005; Penn & Potts, 1999; Tregenza & Wedell, 2000; Zeh & Zeh, 1997). Given that the immune gene complementarity hypothesis assumes that variation in immune coding alleles mediate individual mating preferences, it predicts that individuals selecting mates (discriminators can be female or male) ‘predict’ which of their potential mates should enable them to produce more viable offspring (Gowaty et al., 2007). Therefore, complementary genes hypotheses do not assume that all discriminators will prefer a single best phenotype in a mate. Instead, these hypotheses predict that mating preferences will be self-referential, as the best mate for one discriminator is unlikely to be the best mate for other discriminators (Bluhm & Gowaty, 2004a,b; Downhower et al., 1983; Gowaty et al., 2007). Complementary genes hypotheses thus provide a way for genetic variation to be maintained in the population even in the face of strong mating preferences.

Past studies designed to test the immune gene complementarity hypothesis tested preferences of male and female discriminators, then randomly paired half the discriminators with their behaviourally preferred partners and the other half with their nonpreferred partners, and then quantified offspring viability (reviewed in Gowaty, 2008). The offspring of discriminators that mated with their preferred partners had significantly higher viability than the offspring of discriminators that mated with their nonpreferred partners in ducks (Bluhm & Gowaty, 2004a,b), fruit flies (Anderson, Kim, & Gowaty, 2007), mice (Drickamer, Gowaty, & Holmes, 2000; Drickamer, Gowaty, & Wagner, 2003; Gowaty, Drickamer, & Schmid-Holmes, 2003; Raveh et al., 2014), cockroaches (Moore, Gowaty, & Moore, 2003) and fish (Sandvik, Rosenqvist, & Berglund, 2000; reviewed in Gowaty et al., 2007). These studies support the crucial indirect fitness benefits prediction that offspring of individuals experimentally mated with their preferred partners were healthier and survived longer than the offspring of individuals experimentally mated with their nonpreferred partners.

In all aforementioned experiments performed to date to test the immune gene complementarity hypothesis, the investigators were blinded to variation in elaborate sexual traits or morphology of subjects, as they intentionally picked individuals (discriminators and discriminatees) for inclusion in each experiment at random with respect to their phenotypic characteristics. Furthermore, the investigators did not conduct pre- or postexperimental evaluations of elaborate trait variation among potential mates (but they argued that such tests should be the next step). The investigators utilized this approach because they were motivated by a desire to ascertain whether individuals that were constrained to breed with their nonpreferred partners would produce offspring with lower viability, not by a desire to explain whether morphological or elaborate trait variation influenced offspring survival or reproduction. The investigators were therefore unable to determine whether the result of higher offspring viability might stem from females associating with males with more elaborate traits and/or from females associating with males with more complementary genes (but they argued that combining these ideas should be the next step).

Here we used Jamaican field crickets, *Gryllus assimilis*, to simultaneously test the two indirect fitness benefits hypotheses that have been introduced to explain the evolution of female mating preferences. The ‘good genes’ hypothesis predicts that (1) males with more elaborate traits (e.g. the biggest males and/or the loudest, brightest, most complex, or highest-effort signallers) are healthier and carry fewer pathogens and parasites than males with less elaborate traits; (2) that females prefer to mate with males that have the best health-predictive elaborate traits; and (3) female preference positively affects offspring fitness. Conversely, the ‘complementary genes’ hypothesis predicts that (1) mate preferences are self-referential and therefore not necessarily correlated with traditionally measured phenotypic traits (e.g. size and/or elaborate traits) and (2) when females mate with their preferred partners, their broods have higher egg-to-adult survival (viability). These two hypotheses primarily differ in whether elaborate male traits predict indirect fitness benefits: with good genes, they do; with complementary genes, they do not.

Field crickets are appropriate organisms to test these two hypotheses because (1) females use male acoustic mate attraction signals to distinguish between potential mates and (2) females assess relatedness between potential mates. Field cricket males raise their forewings and rub them together, with each closing stroke producing a pulse of sound. Males concatenate these pulses