



Parasitoid infestation changes female mating preferences

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Females often adjust their mating preference to environmental and social conditions. This plasticity of preference can be adaptive for females and can have important consequences for the evolution of male traits. While predation and parasitism are widespread, their effects on female preferences have rarely been investigated. Females of the cricket *Gryllus lineaticeps* are parasitized by the parasitoid fly *Ormia ochracea*. Infestation with fly larvae substantially reduces female life span and thus reproductive opportunities of the cricket. Both female *G. lineaticeps* and flies orient to male song and both prefer male songs with faster chirp rates to songs with slower chirp rates. We tested the effect of parasitic infestation on female responsiveness to male song and female chirp rate preferences. The proportion of individuals responding to male songs did not differ between infested and control females. Control females preferred intermediate chirp rates to slow chirp rates and did not discriminate between fast and intermediate chirp rates. In contrast, infested females showed no preferences in the choice trials, indicating reduced chirp rate selectivity. This plasticity in female preferences may be adaptive; parasitized females may have a higher probability of reproducing before they are killed by the parasitoids if they are less selective (i.e. there will be a larger pool of males considered acceptable). The change in preferences suggests relaxed selection on male chirp rate during times of parasitism.

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Female mating preferences often show substantial plasticity and change in response to a variety of biotic environmental factors, such as predation (e.g. Hedrick & Dill 1993; Godin & Briggs 1995; Gong & Gibson 1996; Johnson & Basolo 2003), parasitism (e.g. Zuk et al. 1990; Poulin 1994; Cordoba-Aguilar et al. 2003) or social experience (e.g. Wagner et al. 2001b; Hebets 2003; King et al. 2003). Because plasticity in female preferences can change the strength and direction of sexual selection, it can have important ramifications for the evolution of sexually selected male traits (Poulin & Vickery 1996; Rolff 1998; Cotton et al. 2006). For example, a reduction in selectivity allows males that usually are rejected by females to obtain matings under some environmental conditions, which may help to maintain genetic and phenotypic variation of male sexually selected traits (Chaine & Lyon 2008).

The effect of parasitism on female preferences is particularly understudied, despite evidence that parasitism can have major effects on host reproduction and behaviour. For example, parasitic infestation may cause sex-role reversals (Simmons 1994) and changes in reproductive patterns and behaviour (e.g. Baudoin 1975; Ritchie & Høeg 1981; Rupp 1996; Zakikhani & Rau 1999; Beckers &

Wagner 2011b) and in nonreproductive behaviour (e.g. Moore 1995; Libersat et al. 2009). Some studies have also shown that parasitism can affect female mate sampling (Buchholz 2004) and mate choice (Poulin & Vickery 1996; Cordoba-Aguilar et al. 2003; Mazzi 2004). Even though parasitism and predation are prevalent in many taxa, parasite or predator-mediated changes in male traits, and especially female preferences for those traits, have received relatively little attention in studies of animal behaviour (Poulin 1994).

Males of the variable field cricket, *Gryllus lineaticeps*, produce songs to attract females for mating. Females typically prefer males that produce songs with faster chirp rates (Wagner 1996), although they discriminate more strongly between low and intermediate chirp rates than between intermediate and high chirp rates (Wagner & Basolo 2007a; Beckers & Wagner 2011a). Males that produce faster chirp rates provide direct benefits to females that increase female fecundity and fertility in low nutrition environments (Wagner & Harper 2003; Tolle & Wagner 2011). Male calling song, however, not only attracts conspecific females, but also a parasitoid fly, *Ormia ochracea*, which deposits about 3 larvae on and 7 larvae around the male (Adamo et al. 1995a). Males are infested by larvae deposited directly on their body (Cade 1975). Silent females can be infested in a more indirect fashion: females that approach a singing male for mating may pick up the sticky larvae deposited around the male (sensu Cade 1975; Martin & Wagner

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2010), or they may be infested if they are in close proximity to the male when he is attacked by the parasitoid fly. In the field, infestation rates of *G. lineaticeps* can be as high as 60% for males and 6% for females (Martin & Wagner 2010). Infestation is typically always lethal for the host, and the host dies within 7–10 days of infestation (Adamo et al. 1995b; Beckers & Wagner 2011b). Infested males substantially reduce their singing within 1 day after infestation (Beckers & Wagner 2011b). In other species of *Gryllus*, females that were infested with *O. ochracea* larvae showed reduced reproductive behaviour (e.g. reduced tendency to mount males, rapid decline in egg laying) beginning at 3 days after infestation (Adamo et al. 1995b). Female field crickets typically become receptive to mating around 7 days of adult age and have a maximum natural adult life span of about 28 days (Murray & Cade 1995). Because *G. lineaticeps* females mate with many males throughout their lives (Wagner et al. 2001a, 2007) and reproductive activities begin to decline 3 days following parasitism (Adamo et al. 1995b), infestation can substantially reduce female lifetime reproductive success, particularly for young and intermediate-aged females.

We tested the effect of infestation by *O. ochracea* larvae on female responsiveness to male song and female chirp rate preferences in *G. lineaticeps*. We hypothesized that parasitized females would show adaptive phenotypic plasticity in reproductive behaviour by increasing their responsiveness to male song and/or expressing weaker chirp rate preferences. Both changes in behaviour should lead to an increase in the probability that a parasitized female will find an acceptable mate and thus reproduce before dying. However, other outcomes for female responsiveness and chirp rate preferences are possible. For example, reduced responsiveness to male song may suggest parasitic manipulation. By preventing the host from reproducing, parasitoid larvae may force the host to save energy that the larvae could use for their own development, and reduce the risk of predation or superparasitism (i.e. infestation of a previously infested host by a member of the same parasite species; sensu van Dijken & Waage 1987). Similarly, reduced responsiveness to male song may be a by-product of infestation (i.e. sick females may not behave like healthy gravid females). As with the adaptive plasticity hypothesis, the parasitic manipulation and by-product hypotheses predict that parasitized females will be less selective. First, high selectivity would prolong female mate searching, which would reduce the host's energy reserves and increase exposure to predators and parasites, which could be detrimental to the larvae. Second, sick females might be less selective because they have fewer resources to devote to sampling males.

METHODS

Animals

We collected adult female *O. ochracea* at Rancho Sierra Vista in the Santa Monica Mountain National Recreation Area (near Newberry Park, CA, U.S.A.) in the summer of 2011, using broadcasts of *G. lineaticeps* song (Wagner & Basolo 2007b; Beckers & Wagner 2011b, 2012a). We collected adult female *G. lineaticeps* from Cayucos, California (35°28'23.16"N, 120°52'16.68"W) in the summers of 2008 and 2009 to establish laboratory populations. The fly *O. ochracea* uses this population of *G. lineaticeps* as hosts for its larvae (Beckers & Wagner 2012b). We brought flies and crickets to the University of Nebraska–Lincoln for the experiments. Most of the female crickets mated with males in the field and laid fertilized eggs in the laboratory. The offspring of the field-collected females constituted the first laboratory generation. We actively managed pairings between males and females for subsequent laboratory generations to reduce inbreeding (Beckers & Wagner 2011a). We

used females of the second and older laboratory generations in our experiments (for rearing protocols see Beckers & Wagner 2011a).

Infestations

Female crickets were reared to adulthood and placed in individual containers. Since female crickets are silent, larval infestation of females most likely occurs either when the female is close to the male as the parasitoid fly attacks the male, or when the female approaches the male for mating and picks up the larvae deposited around the male by the fly. Infestation of females is strongly linked to mating with a male (i.e. virgin females are unlikely to be parasitized). In addition, female *G. lineaticeps* mate with many males throughout their lives (Wagner et al. 2001a, 2007). To simulate the natural course of parasitism (parasitism of mated females), we paired each of our experimental females with one male prior to infestation or 'mock-infestation' (see below). Females were paired with a male 7–17 days after eclosion, and the duration of the pairing was 48 h. On the day that males were removed from the container, we infested approximately half of the females with two fly larvae. To obtain the larvae, we killed a fly, dissected its abdomen and removed live planidia larvae for infestation. We deposited the larvae on the membranous area between head and thorax (Vincent & Bertram 2009) using a probe (for details of infestations see Beckers & Wagner 2011b). The remaining females were mock-infested (i.e. treated exactly the same way as the infested females except that we did not place larvae on the tip of the probe). Two days after infestation or mock-infestation, we tested female chirp rate preferences. Our research adhered to the ASAB/ABS guidelines for the use of animals in research, the legal requirements of the U.S.A., and all guidelines of the University of Nebraska.

Experimental Set-up and Protocol

Females from each treatment group were tested once in one of two choice experiments: (1) slow chirp rate (1.8 chirps/s) versus intermediate chirp rate (3.0 chirps/s), or (2) intermediate chirp rate (3.0 chirps/s) versus fast chirp rate (4.2 chirps/s). These chirp rates approximately cover the natural chirp rate range (mean \pm 2 SD) of male *G. lineaticeps* songs (Wagner & Reiser 2000; Wagner & Basolo 2007a). Note that preferences for faster chirp rates are strongest at the slow-to-intermediate chirp rate range, and females discriminate less strongly between faster chirp rates (Beckers & Wagner 2011a; Wagner & Basolo 2007a). Thus, we expected females to express preferences in the choice test with the slow and intermediate chirp rates rather than in the choice test with the intermediate and fast rates. A given female was only tested with one pair of stimuli. All stimuli were identical in all other song parameters except for the chirp interval (the period of silence between chirps), which was manipulated to generate stimuli that varied in chirp rate (for details see Wagner & Basolo 2007a, b). All stimulus parameters corresponded to natural song values. Each stimulus was calibrated to a peak amplitude of 70 ± 1 dB SPL (re: 20 μ Pa) at a distance of 30.5 cm from the loudspeaker. The infested females used in the two chirp rate trials were drawn from 11 and 14 full-sibling families. The control females used in each of the two chirp rate trials were drawn from 12 and 13 full-sibling families. No more than three females from the same family were included in any chirp rate trial. Linear mixed models that included family as a random effect showed that family had no effect on female responsiveness or choices. Family was therefore excluded from further analysis.

We conducted choice trials with female *G. lineaticeps* on the floor of a semianechoic chamber. We used a video camera inside the chamber and a monitor outside the chamber to observe female

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