



Level up: the expression of male sexually selected cuticular hydrocarbons is mediated by sexual experience



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The use of cuticular hydrocarbons (CHCs) in species recognition, sex identification and sexual selection is widespread in insects. However, few studies have studied plasticity in CHCs. Here we examine the effect of age and social environment on a suite of sexually selected CHCs in *Drosophila serrata*. We demonstrate that the combination of CHCs that is associated with increased male mating success (CHC β) changes as males age, and this effect is mediated by social environment. When single males were housed with multiple females, their expression of CHC β increased across the first few days of their adult life, after which expression declined with increasing age. In contrast, sexually selected CHCs of males housed with other males, males housed with other males and females, and males housed alone all decreased across days. To determine the long-term consequences of mating on CHC expression, we allowed males a single mating opportunity and subsequently found some indication of a brief spike in CHC β . Finally, to determine whether visual and olfactory contact with females, copulation, or intromission causes males to express high values of CHC β , we manipulated male access and physical contact with females. We found that although prolonged copulation causes a slight increase in male CHC β , only a successful copulation with sperm transfer induced males to develop CHCs associated with high mating success. Taken as a whole, our results demonstrate that the expression of sexually selected CHCs in males varies with both age and social context, and suggest that the latter is mediated at least in part by successful matings with females. More generally, contextual plasticity in CHCs is likely to affect both the experimental design of CHC-based experiments and the evolution of CHC signals as naturally and sexually selected traits.

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Cuticular hydrocarbons (CHCs) are long-chain, largely nonvolatile waxes that are produced by oenocyte cells on the cuticle of most insects (Antony & Jallon, 1982; Wigglesworth, 1970). CHCs serve to reduce water loss through the cuticle and thus protect against desiccation (Foley & Telonis-Scott, 2011; Gibbs, Fukuzato, & Matzkin, 2003; Howard & Blomquist, 2005). In many species, CHCs and their derivatives containing various functional groups have been secondarily co-opted as a means of chemical communication and have been shown to function in species recognition (e.g. Alves et al., 2010; Buellesbach et al., 2013; Maroja et al., 2014), sex recognition (e.g. Antony & Jallon, 1982; Chenoweth & Blows, 2003, 2005), and as a means to discriminate among individuals within a population. With respect to the latter, CHC profiles are involved in recognizing previous mates (Weddle et al., 2013), in recognizing

nestmates (Marten, Kaib, & Brandl, 2010; Ozaki, Kidokoro-Kobayashi, & Hiraguchi, 2012), and as a means of nest marking (Lorenzi, Cerro, & Bagnères, 2011). Specific combinations of CHCs have been associated with mate choice in both males and females (Chenoweth & Blows, 2005; Hunt, Snook, Mitchell, Crudgington, & Moore, 2012), and in some cases serve to mediate male–male competition (Thomas & Simmons, 2009).

Unlike the long-range mate attraction pheromones of moths and beetles that tend to have just one or a few dominant compounds that are perceived by the receiver, CHCs are often substantially more complex, being composed of multiple different alkanes, alkenes and methyl-branched hydrocarbons (Ferveur & Cobb, 2010). Furthermore, an individual's CHC profile can vary in response to factors such as diet (Fedina et al., 2012), desiccation stress (Stinziano, Sové, Rundle, & Sinclair, 2015) and age (Kuo et al., 2012). Social environment can also influence CHC expression in males and females (Farine, Ferveur, & Everaerts, 2012; Kent, Azanchi, Smith, Formosa, & Levine, 2008; Petfield, Chenoweth, Rundle, & Blows, 2005). These changes in CHC expression suggest

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that male CHC expression may exhibit contextual plasticity, defined as ‘variation in an individual’s behaviour as a function of variation in the external stimuli (context) at the time the individual expresses that behaviour’ (Ord, Stamps, & Losos, 2010, page 3135). Furthermore, these instances of contextual plasticity in CHC expression may potentially be beneficial to the male, although this has been addressed in surprisingly few studies (but see Thomas & Simmons, 2009, 2011).

In *Drosophila serrata*, an Australian species of fruit fly, CHCs have been studied extensively, with the majority of work (over 40 publications to date) focusing on their role as contact pheromones that are used in species recognition and during mate choice within populations (Blows & Allan, 1998; Chenoweth & Blows, 2003, 2005). Males and females express the same set of nine compounds, although their relative concentrations are sexually dimorphic. Both sexes also use these traits when choosing mates, although the preferred blend, and the form of sexual selection (e.g. directional, stabilizing), vary between males and females (Chenoweth & Blows, 2005; Rundle & Chenoweth, 2011). CHC appear costly to produce (Blows, 2002) and their expression in males is condition dependent (Delcourt & Rundle, 2011). Both CHCs and female preferences for them have a genetic basis and have been shown to respond to altered selection (Blows, 1998; Delcourt, Blows, & Rundle, 2010; Higgie, Chenoweth, & Blows, 2000; Hine, McGuigan, & Blows, 2011; Rundle, Chenoweth, & Blows, 2009; Rundle, Chenoweth, Doughty, & Blows, 2005). Consequently, *D. serrata* has also been used as a model system to examine hypotheses about the genetic architecture of multivariate, sexually selected traits.

In a recent paper we characterized short-term temporal changes of *D. serrata* CHC expression and plasticity of these changes in response to different social environments. We showed that when individuals were housed alongside others, the CHCs of both males and females varied across a 24 h period in an apparent circadian pattern. Focusing on the combination of CHCs targeted by sexual selection (termed CHC β), males had higher values when housed under social conditions that provided greater access to females (and hence greater opportunity for mating), and their value peaked during the time of day when matings were most common. In both cases, these contextual changes in CHCs should enhance mating success (i.e. because males express higher values of the trait combination favoured by sexual selection), suggesting adaptive plasticity (Gershman, Toumichey, & Rundle, 2014b).

Building on this previous work, here we quantify longer-term changes (i.e. across days) in CHC expression over the early lives of males and the effects of social environment on CHC expression. Oenocyte cells mature over the first week after adult eclosion (Johnson & Butterworth, 1985), with both male and female *D. serrata* becoming sexually competent approximately 36 h after adult eclosion (S. N. Gershman & H. D. Rundle, personal observation). Our study has three parts. First, we characterized how the combination of CHCs targeted by sexual selection changes over the first week in adults, and we manipulated social environment to investigate its effects on this. In the second part, we tested the effect of mating on the expression of male sexually selected CHCs. Our interest here concerned whether and how a single mating may alter CHC expression across days. However, this assay also provided a test of a fundamental assumption of all sexual selection analyses that have been done using binomial mate choice trials in *D. serrata*: that the act of mating itself does not alter CHCs prior to their extraction (e.g. due to physical transfer or as a by-product of physiological changes induced by mating). Changes in CHCs induced by mating that occur prior to extraction would create a difference between chosen and rejected males that would confound any difference resulting from mate choice (i.e. sexual

selection). Finally, in the third part, we investigated the specific cue that induces males to alter the expression of their sexually selected CHCs in the presence of females.

METHODS

In all assays, we used flies from a previously described laboratory-adapted, outbred stock population of *D. serrata* maintained at large population size (16 half-pint (237 ml) bottles/generation) via nonoverlapping generations (Chenoweth, Rundle, & Blows, 2008; Rundle, Chenoweth, & Blows, 2006). Experimental animals were maintained under constant conditions mirroring that of the stock, including temperature (25 °C) and photoperiod (12:12 h light:dark cycle), with the lights on at 0700 hours and off at 1900 hours daily.

Mating Trials and Identifying Sexually Selected CHCs

To test the effects of time and social environment on male CHC expression, we wanted to focus our analyses on the combination of CHCs that are most strongly associated with increased mating success, thereby reducing a high-dimensional data set to a single trait of biological interest. Our approach to doing this followed established methods that have previously been used in this species (e.g. Gershman, Delcourt, & Rundle, 2014a; Gershman et al., 2014b; Hine, McGuigan, & Blows, 2014; McGuigan, Petfield, & Blows, 2011; Sztepanacz & Rundle, 2012). In brief, we used a series of binomial choice mating trials to calculate the β vector of directional sexual selection gradients (i.e. partial regression coefficients; Lande & Arnold, 1983), equivalent to the linear combination of CHCs associated with highest mating success in males. We extracted and quantified CHCs of males from our experiments (i.e. males varied in age, social experience and mating experience) as described below. Then, we determined an individual’s phenotypic score for the trait combination described by β in a manner identical to calculating an individual’s score for a particular principal component, by using matrix algebra to multiply its measured values by the vector of loadings for that principal component. We calculated this trait, termed CHC β , as $\text{CHC}\beta = \beta^T \mathbf{Z}$, where \mathbf{Z} is the vector of trait values measured on the individual (McGuigan et al., 2011).

As a trait, an individual’s CHC β score represents the individual’s value for the linear combination of CHCs that is most strongly associated with increased male mating success. In previous studies in *D. serrata*, this score has been interpreted as CHC-based ‘attractiveness’ (Gershman et al., 2014a, 2014b; Hine, Lachish, Higgie, & Blows, 2002, 2011), under the assumption that, in the mating trials used to estimate β , variation in male mating success is caused by female mate choice alone. Although *D. serrata* females can choose which males to associate with, and can also dislodge unwanted copulations by shaking off the male (Hoikkala & Crossley, 2000), male–male interactions can also occur during choice trials and may contribute to the outcome. Although *D. serrata* males are not as visibly aggressive to one another as *Drosophila melanogaster* males, if given the opportunity, they will defend a territory and their success at doing so appears to affect their mating success (White & Rundle, 2014). However, CHCs do not appear to be associated with success in male territory defence (White & Rundle, 2014), and the arenas for mating trials used in estimating β were designed to minimize the opportunity for territorial defence (see Gershman et al., 2014b). Nevertheless, it is possible that subtle male–male interactions contribute to variation in male mating success and hence CHC β values. Therefore, we refer to CHC β as ‘male sexually selected CHCs’ and interpret this trait more broadly as the combination of CHCs associated with increased mating success.

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