



Evolution of lure response in tephritid fruit flies: phytochemicals as drivers of sexual selection

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The males of many *Bactrocera* species (Diptera: Tephritidae) respond strongly and positively to a small number of plant-derived chemicals (= male lures). Males that have imbibed the lures commonly have a mating advantage over unfed males, but no female benefits have been demonstrated for females mating with lure-fed males. It has been hypothesized that the strong lure response is a case of runaway selection, where males receive direct benefits and females receive indirect benefits via 'sexy sons', or a case of sensory bias where females have a lower threshold response to lures. To test these hypotheses we studied the effects of lure feeding on male mating, remating and longevity; while for females that had mated with lure-fed males we recorded mating refractoriness, fecundity, egg viability and longevity. We used *Bactrocera tryoni* as our test animal and as lures the naturally occurring zingerone and chemically related, but synthetic chemical cuelure. Feeding on lures provided direct male benefits in greater mating success and increased multiple mating. For the first time, we recorded direct female effects: increased fecundity and reduced remating receptivity. Egg viability did not differ in females mated with lure-fed or unfed males. The life span of males and females exposed to lures was reduced. These results reveal direct, current-generation fitness benefits for both males and females, although the male benefits appear greater. We discuss that while lure response is indeed likely to be a sexual selection trait, there is no need to invoke runaway selection to explain its evolution.

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Male–male competition and female mate choice have long been recognized as important mechanisms of sexual selection across a range of animal species (Darwin 1871; Kirkpatrick 1987). Species-specific attributes associated with sexual selection include body size, male song, courtship displays, visual ornamentation and the presence of antagonistic structures such as antlers (Parker 1970; Boake 1989; Moore 1990; Andersson 1994; Bonduriansky & Rowe 2003; Kortet & Hedrick 2005). Sexual selection may confer direct benefits to the current generation, such as increased fecundity or longevity (Gwynne 1984; Reinhold 1999; Arnqvist & Nilsson 2000), or indirect genetic benefits to the next generation if offspring fitness is increased by the parental female selecting a higher quality mate (Fedorka & Mousseau 2002).

Apart from intrinsic species traits that drive sexual selection, interspecific interactions, such as competition, aggression, avoidance of maladaptive hybridization and predation may cause

selection on secondary sexual characters (Breitburg 1987; Zuk et al. 1998; Stoddard 1999; Marshall & Cooley 2000; Höbel & Gerhardt 2003; Tynkkynen et al. 2005). In insects, interactions with host plants may modify sexual interactions. For example, in both scolytid beetles and arctiid moths, feeding on plant secondary chemicals modifies chemically mediated sexual communications that are associated with mate selection (Landolt & Phillips 1997). In a few tightly coevolved systems some insect species derive unique courtship components as rewards from plants that they pollinate, for example in the well-documented euglossine orchid bees of South America (Zimmermann et al. 2009). Analogous to these examples, but different from them in that coevolution is unlikely for the majority of species involved (Tan & Nishida 2005, 2012), is one possibly unique form of extrinsic influence on sexual selection that involves tephritid fruit flies. In these flies, particularly those of the large genus *Bactrocera* (Diptera: Tephritidae: Dacini), phytochemicals obtained by males from nonhost as well as host plants, which mostly offer no other direct or indirect benefits, are considered a primary modifier of male mating success (Shelly 2010).

The two most commonly studied plant compounds to which male *Bactrocera* respond are methyl eugenol (ME) (4-allyl-1,2-dimethoxybenzene) and cuelure (4-[4-acetoxyphenyl]-2-butanone)

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(Bateman 1972; Metcalf & Metcalf 1992). Methyl eugenol occurs naturally in a wide range of plants, while cuelure does not occur in plants but is a close analogue of several naturally occurring plant chemicals, particularly raspberry ketone (Howlett 1915; Fletcher et al. 1975; Metcalf & Metcalf 1992; Tan & Nishida 2005). Both ME and cuelure elicit strong olfactory and gustatory responses in the males of a wide range of *Bactrocera* species and have been used for many decades for fruit fly surveillance and management practices (Bateman 1972; Cunningham 1989; Seewooruthun et al. 2000). While the functional role of these chemicals to fruit flies was unknown for a long period (Nishida et al. 1988, 1990; Shelly 1995), research over the last 15 years has focused on the influence of these chemicals on mating and sexual selection (Raghu 2004; Shelly 2010). Because these phytochemicals were first used in the context of pest management, they are generally referred to within the fruit fly literature as 'male lures', or simply 'lures', and this generic terminology is used in this paper.

Male lures induce changes in the physiology and possibly the behaviour of male tephritids (Shelly 2010). Male flies that feed on lures transform and store the resultant compounds in their rectal glands, where they are subsequently used for sexual communication (Hee & Tan 2005, 2006). The generally observed pattern is that lure-fed males have a mating advantage over nonlure-fed flies, with that advantage sometimes lasting up to 35 days (Shelly & Villalobos 1995; Raghu & Clarke 2003; Shelly & Nishida 2004; Wee et al. 2007; Shelly et al. 2010); however, this result is not ubiquitous across all species. For example, while male mating advantage in ME-fed *Bactrocera dorsalis* is well documented (Shelly & Nishida 2004), little or no mating advantage (depending on the trial) and no other physiological changes associated with lure feeding were detected for the similarly ME-responsive *Bactrocera cacuminata* (Raghu et al. 2002; Raghu & Clarke 2003). Also, while for some species the male sexual advantage may last for up to a month (Shelly & Dewire 1994), only 1 or 2 days of mating advantage was observed for the cuelure/raspberry ketone-responsive melon fly, *Bactrocera cucurbitae* (Shelly & Villalobos 1995; Shelly 2000a).

While male mating effects are apparent in many of the species studied, any direct effects on females mating with lure-fed males are unknown. Shelly (2000b) found no direct benefits for *B. dorsalis* females that had mated with lure-fed males and, to explain the apparent anomaly of females preferentially mating with lure-fed males, postulated either the 'sensory bias' or 'sexy son' theories. The sensory bias theory hypothesizes that females may also respond to the 'male' lures, perhaps as a mechanism for the location of food or oviposition substrates, but their sensory threshold to the phytochemicals is much lower than that of the males. The response of females to lure-fed males, which are presumably a source of very low concentrations of the chemicals, is thus an artefact of this sensory bias. However, evidence that male lures may act as mate rendezvous stimuli (Raghu & Clarke 2003) suggests that the role of male lures in the mating systems of *Bactrocera* species is more than sensory bias alone (Shelly 2010). In contrast to the sensory threshold hypothesis, the 'sexy son' theory explains the female response to lure-fed males as a result of runaway sexual selection. The sons of females that have mated with lure-fed males should inherit the ability to locate lures in nature, and in turn will be 'sexier' and enjoy enhanced mating success. The parental female thus gains indirect fitness benefits through her sons (Shelly 2000c). However, direct female benefits are required, at least initially, if the 'sexy son' runaway selection theory is to be used to explain the evolution of lure response in fruit flies.

Bactrocera tryoni is a polyphagous fruit fly and the major insect pest of horticulture in Australia (Clarke et al. 2011). Both sexually mature males and sexually mature but unmated females of this species respond to cuelure (Weldon et al. 2008). *Bactrocera tryoni* is considered to exhibit a lek mating system, in which aggregated

males commence rapid wing movements associated with dispersion of a pheromone during dusk, when light intensity drops below a critical level. Subsequently, females approach calling males and copulation ensues (Tychsen 1977). In common with other *Bactrocera* species, we suspect male-attracting phytochemicals to be involved in the mating system of this species, but no previous work on this has been published. Understanding the response of *B. tryoni* to cuelure is important not only for a broader understanding of lure response in fruit flies, but also because it has a strategic value for the future pest management of this fly. As cuelure is a synthetic compound it is inappropriate to focus solely on this chemical when pursuing an evolutionary explanation for the lure response; examining natural compounds to which these flies will have been exposed over evolutionary time is also critical. Several cuelure-responsive *Bactrocera* species are known to respond to zingerone, the essence of ginger found in orchid blossoms, which attracts both cuelure- and ME-responsive flies (Tan & Nishida 2007). In the field, *B. tryoni* responds to zingerone, although its response to cuelure is significantly stronger (Fay 2012). We thus used both cuelure and zingerone in this study to compare the effects of a synthetic and naturally occurring chemical.

In the context of sexual selection and the evolution of lure response, the aims of this study were to investigate: (1) male effects of lure feeding as measured by mating success, time to initiate mating (= copula latency), mating duration, remating levels and longevity; and (2) female effects after mating with lure-fed males as measured by the level of multiple mating, fecundity, egg viability and longevity. Specifically, we tested the prediction, developed from both the 'sexy son' and 'sensory bias' hypotheses, that lure feeding in *B. tryoni* should provide direct mating benefits to males, but with no direct benefits to females mated with lure-fed males. In contrast, should we record direct benefits to females that preferentially mated with lure-fed males, then both hypotheses are invalidated for this species and a traditional sexual selection model, in which benefits to both males and females are observed (Andersson 1994; Møller & Jennions 2001), would be sufficient to explain the evolution of the lure response.

METHODS

Insect Rearing and Holding

Bactrocera tryoni were obtained from an annually refreshed culture maintained by the State Department of Agriculture, Fisheries and Forestry, Brisbane, Queensland, Australia. Flies were provided with protein hydrolysate, sugar and water ad libitum, and maintained at 27 °C and 70% relative humidity in a room illuminated with fluorescent tubes between 0700 and 1600 hours and with natural light for the rest of the day. Stock cultures were held in screen cages (90 × 60 cm and 60 cm high), while experimental colonies were held in smaller Perspex cages (30 × 20 cm and 20 cm high). All experiments were run in these smaller Perspex cages fitted with a cloth sleeve. Colony rearing followed the procedures of Heather & Corcoran (1985). When virgin flies were required, females and males were separated within 2 days after emergence.

Male Effects

Mate selection

Our first aim was to test for evidence of direct male mating benefits afforded by either cuelure or zingerone feeding. Sexually mature (14-day-old) virgin males were exposed to their respective lures and mating observations were done at 0, 1, 3, 7, 14, 21 and 28 days after lure exposure. Lure feeding was achieved by offering males 2 h of unrestricted access to 1.5 ml of cuelure (99%) or 1.5 ml

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