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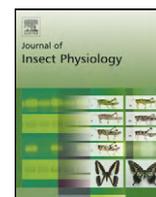
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Enhancing male sexual success in a lekking fly (*Anastrepha suspensa* Diptera: Tephritidae) through a juvenile hormone analog has no effect on adult mortality

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ABSTRACT

While defending lek-territories, male *Anastrepha suspensa* (Loew) produce chemical, acoustic and visual courtship signals. In the laboratory and under semi-natural conditions, topical application of the juvenile hormone analog methoprene doubles pheromone production and subsequently doubles sexual success. However, sexual signals and interactions are likely to be physiologically expensive and so result in higher male mortality. Comparison of males kept in isolation for 35 days, but provided daily with a potential mate or a rival male, revealed that both male- and female-interactors shortened focal-male lifespan. In addition, focal males were either treated with methoprene or not, then either provided with protein in their sucrose-based diet or not. Protein proved to similarly double sexual success and also resulted in longer male life spans in all of the interactor-categories. However, there was no evidence that methoprene induced hypersexuality resulted in higher rates of mortality, i.e., the longevity of males treated with methoprene did not significantly differ from untreated males in the same interactor/diet categories. This apparent lack of costs to a putatively sexually selected signal is unexpected but presents an opportunity to increase the sexual competence of sterile flies with few consequences to their survival following mass-release.

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1. Introduction

Tephritid fruit flies infest hundreds of species of fruits and vegetables and are responsible for trade restrictions wherever they occur (Siebert, 1999). Of particular importance in the New World are the Mediterranean fruit fly (=medfly), *Ceratitidis capitata* (Wiedemann), and species of *Anastrepha*, i.e., the Mexican fruit fly, *Anastrepha ludens* (Loew), the West Indian fruit fly, *Anastrepha obliqua* (Macquart), the South American fruit fly, a complex of cryptic species near *Anastrepha fraterculus* (Wiedemann), the guava fruit fly, *Anastrepha striata* (Schiner) and the Caribbean fruit fly, *Anastrepha suspensa* (Loew) (White and Elson-Harris, 1992). Despite the importance of *C. capitata* to export economies, *Anastrepha* spp. are considered of even greater local significance throughout Latin America and the Caribbean (Aluja, 1994). Where they occur in the United States, expensive suppression (e.g., Caribbean fruit fly in Florida [Riherd and Jenkins, 1996]) or periodic eradication programs (e.g., Mexican fruit fly in Texas and California [Thomas et al., 1999]) are required to allow citrus exports to other states and countries.

Traditional *C. capitata* and *Anastrepha* spp. area-wide control consists of baitsprays, containing a protein-based attractant/food source and an insecticide, formerly Malathion but increasingly Spinosad (Burns et al., 2001). In large-scale eradication programs these sprays are followed by repeated mass-releases of sterile males (e.g., Rull et al., 1996). Despite the decades long use Sterile Insect Technique (=SIT) to control *C. capitata* there is considerable room for improvement, both in terms of rearing and effectiveness of sterile males in the field (e.g., Shelly et al., 2003). Part of the reason that SIT often fails to reach its theoretical potential is that sterilizing irradiation harms the performance, including male sexual performance, of released insects (e.g., Barry et al., 2003). Decreased sterile male capacity may be a particular problem in tephritid SIT programs because of their often complex lek-based mating systems in which male territoriality and female mate choice play important roles. In *A. suspensa*, lekking males produce relatively large amounts of pheromone (Teal et al., 2000), and this emission is accompanied by frequent bouts of wing fanning that both generates an acoustic signal and presumably disperses the volatile chemicals (Sivinski et al., 1994). Signaling occurs daily over a period of several hours on leaf-territories defended from other males (Burk, 1983, 1984; Sivinski, 1989).

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Several means of improving mass-reared tephritid male sexual success have been developed, including exposure to various plant volatiles (“aroma-therapy”, Shelly et al., 2003), application/consumption of the juvenile hormone analog methoprene (Teal et al., 2000) and providing dietary protein in adult diets (Faria et al., 2008). The latter two methods have been particularly effective in *Anastrepha* spp. (Pereira, 2006; Pereira et al., 2009, 2010) and in the case of methoprene treatment the increase in male attractiveness is thought to be due to a doubling of the amount of pheromone produced (Teal et al., 2000). In theory, there should be a physiological cost to sexual activity (e.g., Hunt et al., 2004; Harshman and Zera, 2006). Sexually active *A. suspensa* (Sivinski, 1993), *C. capitata* (Papadopoulos et al., 2010) and *Drosophila melanogaster* L. males (Cordts and Partridge, 1996) do not live as long as those that are never given opportunities to mate. While there are numerous instances of males, including tephritid males (Papadopoulos et al., 2004), that signal relatively more and also live relatively longer (Jennions et al., 2001), this is believed to be due to underlying physical/genetic qualities that are positively correlated to both signaling and longevity. If males could be manipulated to signal at rates independent of their capacities, then the costs of the signals would presumably emerge and these relationships evaporate. Among the potential costs leading to greater mortality are: (1) the materials and energy used to produce signals, such as pheromones; (2) physical damage in agonistic interactions; (3) materials and energy lost due to agonistic interactions; and (4) materials and energy lost due to copulation and substances/gametes transferred to females during copulation. These costs would be predicted to be even greater in males with enhanced sexual activities. If so, the extent of the physiological price paid would influence the usefulness of enhancement techniques. For example, if methoprene and/or protein treatments lowered adult male lifespan to a certain point they may not be useful in SIT programs.

To determine if signaling and sexual/agonistic encounters were an important component of sexually active male *A. suspensa* mortality we controlled access to mates and competitors and to nutritional resources as well as manipulating the level of signal production. We used two ways to increase signaling and subsequent copulations, protein enrichment of adult diet and the topical application of the juvenile hormone analogue, methoprene (Teal et al., 2000; Pereira, 2006). Both significantly increase ($\sim 2\times$) male sexual success by increasing lek participation, territory defense, rate of female encounters, and ratio of female acceptance per encounter (Pereira et al., 2009, 2010). The effects of these two treatments are generally similar, and when combined are additive ($\sim 4\times$ more sexual success than untreated males; Pereira et al., 2010).

Specifically, if the pheromone signal/sexual and agonistic interactions were expensive, and this expense was reflected in increased mortality, then we would predict the following: (1) the repeated addition of another fly would decrease longevity in focal flies (there was no *a priori* reason to predict that a decrease would be greater in the presence of either males or females, although male–male interactions may be more frequent in the wild because of male-biased sex ratios at lek sites, Sivinski, 1989); (2) increased signaling due to methoprene treatment would shorten life span regardless of conspecific interactions; (3) protein treatment would shorten life spans due to increased signaling regardless of conspecific interactions, but perhaps to a lesser extent than methoprene because of its possible counteracting nutritional advantages; and (4) males treated with JH and protein ($\sim 4\times$ increase in sexual success) would not live as long as males given protein but no methoprene ($\sim 2\times$ increase), i.e., males with enriched nutrition would still be affected by the signaling costs of methoprene treatment.

2. Methods

To evaluate the costs of the different aspects of male reproduction, we measured longevity in individually caged males exposed to the various combinations of the following treatments and their respective controls: (1) daily exposure to either another male or a female; (2) topical application of the juvenile hormone analogue methoprene (M^+) which increases sexual activity and success; and (3) providing protein (P^+) added to the diet which physiologically supports reproductive interactions and increases sexual activity and success.

2.1. Insects

A. suspensa used in the study was obtained from a laboratory colony at the Center for Medical, Agricultural and Veterinary Entomology (CMAVE), USDA-ARS, at Gainesville, FL. The colony had been in existence for less than 3 years and was maintained according to an established mass rearing protocol (FDACS, 1995). Flies to be used in experiments were obtained from pupae sorted into weight classes. This was done to eliminate any impact of size variance on male competitiveness. Males weighed an average of 10.9 ± 0.7 mg ($n = 30$), and females an average of 11.9 ± 0.8 mg ($n = 30$). These pupal weights are in the middle range of *A. suspensa* pupae collected from infested fruits in nature (Sivinski, 1993; Sivinski and Calkins, 1990). After emergence and during experiments, the flies were maintained in a laboratory room with a photoperiod of 13L:11D (light from 7:00 to 20:00), with light intensity of 550 ± 50 lx, temperature of 25 ± 1 °C and relative humidity of $55 \pm 5\%$.

2.2. Treatments

In order to more fully reveal the roles of resource expenditure, particularly the intensity of sexual signals and rates of sexual interactions, and resource availability on male survival, juvenile hormone (methoprene) and dietary protein levels were manipulated. The following treatments were compared within the experimental groups of males described below:

- application of juvenile hormone analog, methoprene (M), and sugar and hydrolyzed yeast (protein source) as adult food (M^+P^+);
- methoprene application and sugar as adult food (M^+P^-);
- no methoprene application and sugar and hydrolyzed yeast as adult food (M^-P^+);
- no methoprene application and sugar as adult food (M^-P^-).

Methoprene, a synthetic juvenile hormone analog, was applied topically in the first 24 h after adult emergence at a rate of $5 \mu\text{g}$ in $1 \mu\text{l}$ acetone solution per male in M^+ treatments. In M^- treatments, $1 \mu\text{l}$ of acetone was applied, to serve as a control. Males were immobilized in a net bag and the solution applied via pipette through the net onto the dorsal surface of the thorax. No anesthesia was used to immobilize the flies. Two different net bags and pipettes were used (one for M^+ treatments and other for M^- treatments) to prevent methoprene contamination. In the P^- treatments only water and sugar *ad libitum* were supplied to the flies. In the P^+ treatments hydrolyzed yeast was added to the adult diet as a protein source (mixed with sugar in a proportion of three parts of sugar and one part of hydrolyzed yeast). This mixture is considered a high quality diet for *Anastrepha* species (Jácome et al., 1995; Aluja et al., 2001).

Females used in the experiment were sexed on the first day of adult life and maintained virgin (in the absence of males) with the P^+ diet, i.e., sugar plus hydrolyzed yeast (3:1) and water *ad libitum*.

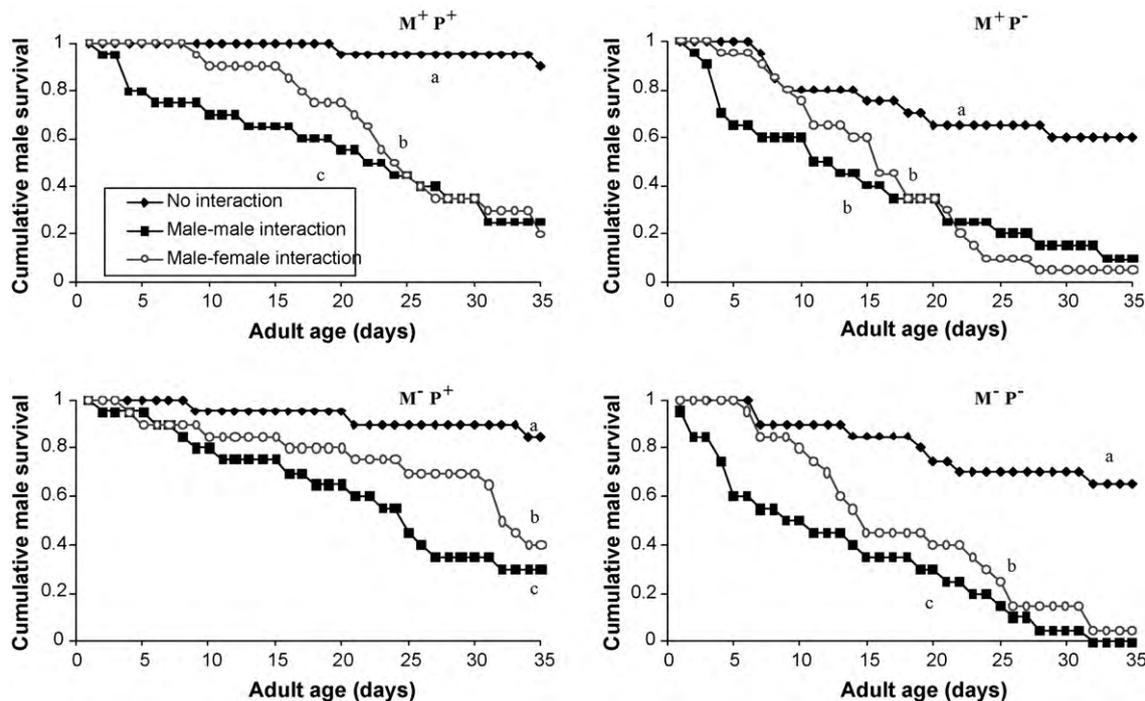


Fig. 1. Cumulative survival probability of male *Anastrepha suspensa* in the three conspecific-encounter groups (a, males alone–no interaction; b, male–male interaction; c, male–female interaction), when treated or not with methoprene (M^+/M^-) and fed or not with protein (P^+/P^-). Lines with the same letter for each treatment were not significantly different (Cox proportional hazard model, $\alpha = 0.05$).

conspecific interactions and this was not supported. Methoprene treated flies survived as long as those that did not receive methoprene treatments (Table 1 and Fig. 2). Prediction #3, that protein treatment would shorten life spans due to increased signaling regardless of conspecific interactions, but to a lesser extent than methoprene because of its counteracting nutritional advantages, was met (Table 1 and Fig. 2). Regardless of conspecific interactions, protein-fed males lived longer than those that were protein-deprived. Prediction #4, that males treated with JH and protein ($\sim 4\times$ increase in sexual success) would not live as long as males given protein but no methoprene ($\sim 2\times$ increase), i.e., males with enriched nutrition would still be affected by the signaling costs of methoprene treatment, was not supported. Regardless of conspecific interactions, males that received methoprene and protein survived as long as those provided with protein alone (Table 1 and Fig. 2). Thus, elevated sexual signaling, in the presence of interactors or in their absence, did not result in greater male mortality and this was true whether or not diets were enriched.

4. Discussion

Females of many species choose mates by comparing males' visual, chemical and acoustic signals. Such preferences often result in certain males obtaining more copulations than their competitors, and this is particularly true in species where signaling males aggregate into leks (Höglund and Alatalo, 1995). The phenomena of male signaling and female mate choice have been frequently documented, but the reasons that females choose certain males or certain male signal suites have been a subject of much discussion (Jennions et al., 2001; see however Koko et al., 2002). While several of the widely proposed theories make different predictions concerning the physiological costs of male signals, all would seem to predict that an increase in signaling alone, without changes in genetic constitution or nutritional state, would have a detrimental effect on male condition and longevity. We tested this prediction by artificially increasing a relatively extravagant male chemical

signal in *A. suspensa*, with methoprene, protein or a combination of both (Pereira et al., 2010). We then examined the consequences of the enhanced signal (through regular interactions with both potential mates and rivals) and observed the effects of higher signal production on male mortality rates.

There was a clear cost to sexual (exposure to females) and agonistic (exposure to males) encounters. The presence of a sexual rival or potential mate resulted in lower male survival, but one presumed cause of this decline, increased signal production and display effort brought about by exposure to methoprene, had no effect on longevity. This is inconsistent with the comparable decline in survival of *C. capitata* males that either signal and mate or signal alone; i.e., the signal and not the contact is the source of increased mortality (Papadopoulos et al., 2010). The present *A. suspensa* results suggest that physiological stresses, and perhaps physical damage, that result from repeated relations with conspecifics were more detrimental to survival than signaling expenses.

Males in the laboratory treated with methoprene appeared to be able to double their signal production/sexual success without immediate consequence, regardless of the quality of their nutritional resources. Given the sexual rewards of such an increase it is reasonable to consider why they have not doubled their efforts without the addition of methoprene (i.e., juvenile hormone). Several explanations could be proposed, two of which were inherent in the experimental design. First, the production of juvenile hormone is a limiting expense in courtship. If so, we subsidized signals with methoprene and made its improvement relatively cost free. However, because juvenile hormone is simply a "messenger" that stimulates reproductive competence and is not directly involved in pheromone synthesis it is not obvious why it should be expensive to produce relatively small amounts. Second, the experiment did not last long enough to discover signaling costs that would have become apparent later in the males' lives. As noted earlier, individually caged male *A. suspensa* has lived as long as 150 days under laboratory conditions (Sivinski, 1993), and age related

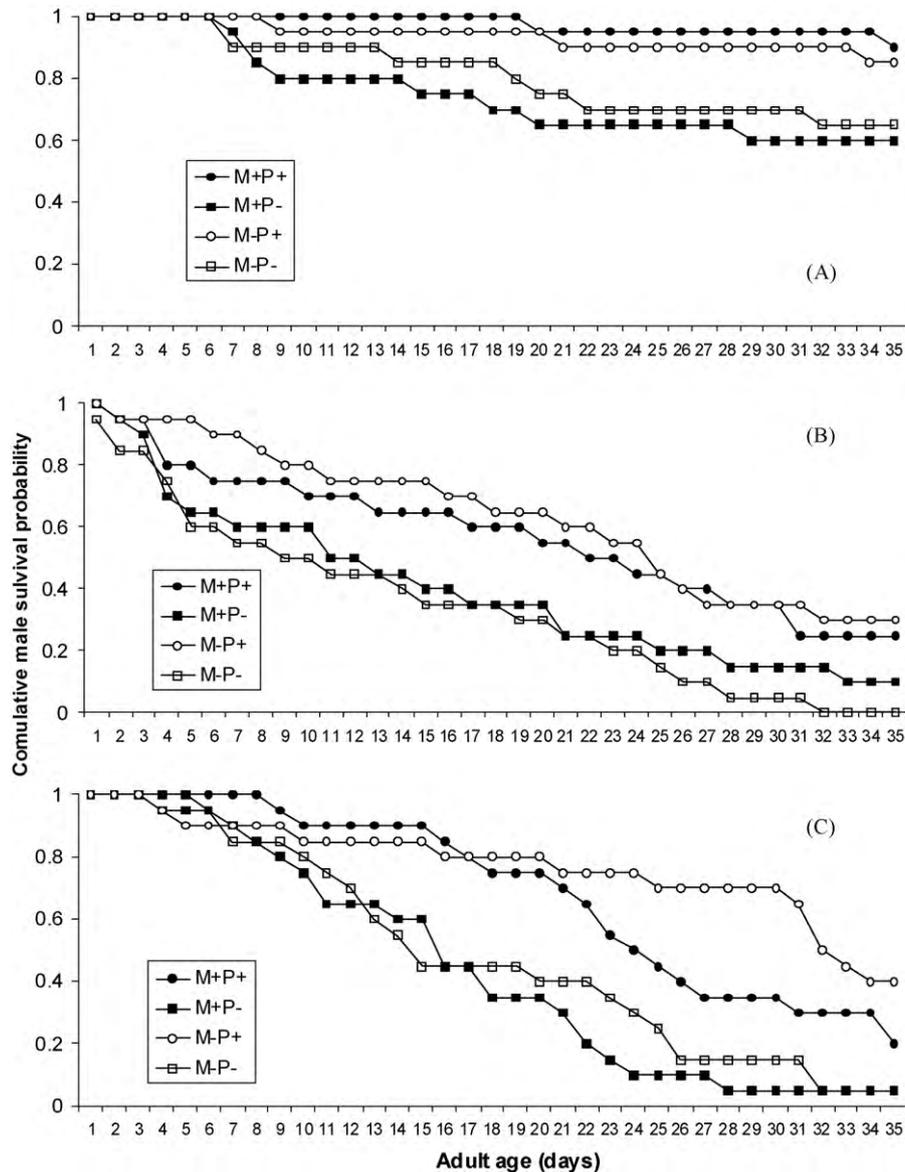


Fig. 2. Cumulative survival probability of male *Anastrepha suspensa* in the four diet/methoprene treatment-groups when exposed daily to either no conspecific (A), a male conspecific (B) or a female conspecific (C). Lines with the same letter for each treatment were not significantly different (Cox proportional hazard model, $\alpha = 0.05$).

changes in mortality rates due to diet and reproductive costs occur in other flies (e.g., Carey et al., 1998). However, in male and female interaction-groups, the majority of males failed to survive for 35 days and this limits the possibility that late-life costs were overlooked.

Alternatively, males may limit their signals and other sexual behaviors not because of physiological expense but because they are costly in some other way. Perhaps displays invite dangers not present in the laboratory (Burk, 1982; Zuk and Kolluru, 1998). There are known risks associated with pheromone production in *C. capitata*. Mediterranean populations of the wasp, *Vespa germanica* are highly attracted to the male pheromone and consume great numbers of signaling males (Hendrichs and Hendrichs, 1998). There are no similar data for *A. suspensa*, but two volatile compounds associated with herbivore-induced leaf damage (β -ocimene and α -farnesene; Effmert et al., 2008), are also present in the sex pheromone (Lu and Teal, 2001) and thus in a position to attract natural enemies (e.g., Whitman and Eller, 1990). If this was the case additional juvenile hormone (methoprene) simply forced males to emit a non-adaptive display whose costs they avoided by

being in the laboratory. However, it is not clear why providing protein has the same effect on sexual success unless well fed males are better able to deal with the consequences of an extravagant signal and so signal more. If so, increased sexual activity would be an adaptive response to a nutritional windfall.

The failure to find immediate costs to enhanced sexuality has implications for *Anastrepha* SIT programs. In the absence of information on costs unobservable in the laboratory, such as increased predation, methoprene treatment appears to offer considerable advantages (Teal et al., 2007). Dietary protein was equally effective in enhancing sexual performance (Pereira et al., 2009, 2010) and increased lifespan as well. The sexual response to protein is similar in *C. capitata* (Faria et al., 2008), although protein's effects on lifespan are somewhat complex and ambiguous (Carey et al., 1998; Yuval et al., 1998; Kaspi and Yuval, 2000; Good and Tatar, 2001; Faria et al., 2008). There are financial costs to the benefits of greater sexual success and longer life, that of diet and hormone supplements and the equipment to incorporate them into rearing procedures. Field trials with sterile males should be performed to determine if the sexual benefits are worth the additional expense.

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