

## CHAPTER 4.5.

# IMPROVING POST-FACTORY PERFORMANCE OF STERILE MALE FRUIT FLIES IN SUPPORT OF THE STERILE INSECT TECHNIQUE

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## SUMMARY

The sterile insect technique (SIT) is being applied against tephritid fruit fly pests in many areas of the world. Currently, fruit fly factories have the capacity to produce and sterilize several billion (thousand million) sterile insects per week, and to make them available for shipment to their final destinations. At sterile fly emergence and release facilities, the emerging flies are fed and held close to maturity, and then collected for area-wide release. While much research effort has been invested in improving mass-rearing and quality-control procedures at the fly-factory level, the post-factory handling of sterile flies has received much less attention. However, research (conducted mainly from 2000 onwards) has focussed on developing and validating ways of improving sterile male performance through better management during a critical period (starting with the arrival of pupae at the fly emergence and release facility and ending with the release of the sterile flies in the field). This chapter summarizes the progress made on this subject for fruit fly species (in the genera *Anastrepha*, *Bactrocera*, *Ceratitis* and *Zeugodacus*) against which the SIT is being applied. To increase the effectiveness of fruit fly SIT programmes, exposure of sterile males to nutritional, hormonal, and semiochemical treatments has been assessed for improvement in sterile male performance, and enhancement of post-factory handling and release methods. Incorporation of protein and juvenile hormone into pre-release *Anastrepha* spp. diets significantly accelerates sterile male maturation and improves sexual performance in several species. Improved or probiotic adult diets and semiochemical treatments using ginger root oil or citrus oils in *Ceratitis capitata*, and methyl eugenol and raspberry ketone in *Bactrocera* and *Zeugodacus* species, significantly increase sterile male mating competitiveness. Some of these treatments and improvements have been transferred to, and are being applied routinely in, operational programmes. However, these efforts need to be further strengthened to assess the interaction among different environmental and holding conditions, treatments and release systems, and to improve further the performance of mass-produced sterile males, a critical component of increasing the effectiveness of operational programmes.

## 1. INTRODUCTION

Application of the sterile insect technique (SIT), as part of an area-wide integrated pest management (AW-IPM) approach against fruit fly (Diptera: Tephritidae) pests, is gaining momentum, with active programmes targeting fruit fly pest species of economic importance in North, Central and South America, Europe, Middle East, Asia, Africa, and Australia (Enkerlin, this volume). There are now fruit fly factories with the capacity to mass-rear several billion (thousand million) sterile male insects per week (for detailed information, note the World-Wide Directory of SIT Facilities (DIR-SIT 2020)) (Parker, Mamai et al., this volume). After irradiation (Bakri et al., this volume), pupae are shipped to their destination, where they are processed in fly emergence and release facilities (FAO/IAEA 2017; Dowell et al., this volume). Several days after emergence, feeding, and sexual maturation, the sterile flies are released in the field, where the sterile males are expected to mate with, and transfer an effective ejaculate to, wild females. An industrial process, consisting of numerous complex steps, is required to achieve a biological goal (Pereira et al. 2013a).

Several quality-control and quality-assurance protocols have been developed to ensure that the released flies fulfil a series of minimum quality standards (FAO/IAEA/USDA 2019; Parker, Vreysen et al., this volume), but exigencies of the industrial process often affect the biological qualities of the final product.

The mass-rearing of fruit flies up to the pupal stage, including sterilization, takes place in specially designed insect factories (where insects are adapted to indoor conditions) (FAO/IAEA 2018). As late-stage pupae, the mass-reared insects are irradiated and shipped to fly emergence and release facilities, where they are placed in containers/release bags, boxes or towers for adult emergence, feeding and holding

before they are released into target field areas (FAO/IAEA 2017; Dowell et al., this volume). During this critical period at these facilities, there is the potential to manipulate sterile males in a manner that will improve their mating success in the field (Pereira et al. 2013a). This includes optimizing the provision of nutritional supplements (Yuval et al. 2002), and hormonal (Teal et al. 2000) and semiochemical treatments (Shelly 2001), as well as the holding conditions and preparations for release (Tween and Rendón 2007; USDA/APHIS 2009; FAO/IAEA 2017).

An FAO/IAEA Coordinated Research Project (CRP) on “Improving Sterile Male Performance in Fruit Fly SIT Programmes” was conducted (2004 to 2009) with the objective of increasing the effectiveness of the SIT by improving the performance of sterile males after mass-rearing. The outcome of this research network, involving 31 research institutes in 17 countries, was summarized by Pereira et al. (2013a). Since then, the fields of applying nutritional, hormonal, and semiochemical treatments, as well as the work on optimizing pre-release conditions and operations that improve male quality, have continued to evolve. This chapter summarizes the current status in improving the performance of sterile males after mass-rearing.

## 2. NUTRITIONAL SUPPLEMENTS

In a majority of tephritid fruit flies, both males and females are anautogenous, emerging as adults with mostly undeveloped gonads. Both sexes rely on foraging during early adult life to ingest carbohydrates to fuel metabolic activities, as well as nitrogenous compounds for gonadal and accessory gland development and pheromone production (Epsky and Heath 1993; Hendrichs and Prokopy 1994). Thus, the survival and reproductive success of males in most tephritid species of economic importance is linked to the access to these nutrients. Nevertheless, several fly emergence and release facilities still do not include nitrogenous compounds in the pre-release diet of sterile males. The sterile males are generally offered a pre-release diet of only sugar or highly concentrated sucrose, presented in agar blocks, which are also a source of water (USDA/APHIS 2009; FAO/IAEA 2017).

The results on assessing nutritional supplements in the last 20 years are described thematically in more detail, together with relevant references, in Table 1. Studies on four genera of tephritids (*Anastrepha*, *Bactrocera*, *Ceratitis* and *Zeugodacus*) indicate that providing yeast hydrolysate to males, as part of the pre-release diet in the days following emergence, can enhance male sexual performance and reduce wild-female remating, although the optimal dosage and most practical form of presentation in an operational context still needs to be refined further (Kaspi and Yuval 2000; Aluja et al. 2001; Pérez-Staples et al. 2007; Haq et al. 2010a, 2014a). The implementation of such a strategy depends on a specific understanding of the nutritional needs of males (while feeding on nitrogenous sources in nature), trade-offs between sexual performance and survival, and operational costs and benefits. Another benefit of providing a protein-enriched pre-release diet is that sterile males will be much less attracted to nitrogenous baits in sprays or traps (such as Biolure or CeraTrap) that are increasingly being used for monitoring wild females when releasing only sterile males (Vargas et al. 2002; Maor et al. 2004; Vargas and Prokopy 2006; San Andrés et al. 2009).

Table 1. Summary of results, by thematic subject, of research conducted on the incorporation of nutritional supplements into pre-release diets and male performance of tephritids of the genera *Anastrepha*, *Bactrocera*, *Ceratitis*, and *Zeugodacus* (modified after Pereira et al. 2013a, reproduced with permission)

Subject addressed	Summary of results
Natural food	<ul style="list-style-type: none"> <li>• Males feeding on orange (<i>Citrus sinensis</i> (L.) Osbeck) or mango (<i>Mangifera indica</i> L.) exhibit modified pheromone composition and improved sexual performance in <i>Anastrepha ludens</i> (Loew) and <i>Anastrepha obliqua</i> (Macquart) (Liedo et al. 2013; Utgés et al. 2013).</li> <li>• Male pheromone production is quantitatively affected by natural food in <i>A. ludens</i> and <i>A. obliqua</i> (Liedo et al. 2013).</li> <li>• Wild <i>Bactrocera tryoni</i> (Froggatt) males feeding on natural sources of food mature much slower than wild males with access to yeast hydrolysate; effects of diet are far less pronounced in mass-reared males (Weldon and Taylor 2011).</li> </ul>
Dietary supplements	<ul style="list-style-type: none"> <li>• Adding yeast hydrolysate (protein) to the pre-release diet significantly improves male sexual performance in <i>Anastrepha fraterculus</i> (Wiedemann), <i>A. ludens</i>, <i>A. obliqua</i>, <i>Anastrepha serpentina</i> (Wiedemann), <i>Anastrepha striata</i> Schiner, <i>Anastrepha suspensa</i> (Loew), <i>Bactrocera correcta</i> (Bezzi), <i>Bactrocera dorsalis</i> (Hendel), <i>B. tryoni</i>, <i>Bactrocera zonata</i> (Saunders), <i>Ceratitis capitata</i> (Wiedemann), <i>Ceratitis quilicii</i> De Meyer, Mwatawala, and Virgilio, and <i>Zeugodacus cucurbitae</i> (Coquillett) (Taylor and Yuval 1999; Aluja et al. 2001; Shelly et al. 2005; Pérez-Staples et al. 2007, 2008b, 2009; Yuval et al. 2007; Pereira et al. 2009, 2010a, b, 2011; Haq et al. 2010a, b, 2013; Haq and Hendrichs 2013; Liedo et al. 2013; Liendo et al. 2013; Orankanok et al. 2013; Quilici et al. 2013; Ndzana et al. 2016; Shelly 2017a).</li> <li>• Adding protein to the pre-release diet improves male weight and body protein content in <i>A. suspensa</i>, <i>B. dorsalis</i>, and <i>Z. cucurbitae</i> (Haq et al. 2010c; Pereira et al. 2011; Reyes-Hernández et al. 2019). It also enhances male sexual organ development in <i>B. dorsalis</i> (Reyes-Hernández et al. 2019) and <i>B. tryoni</i> (Pérez-Staples et al. 2011).</li> <li>• Some studies in <i>C. capitata</i> found no difference between sugar-only fed males and yeast hydrolysate-fed males in terms of mating success (Shelly and McInnis 2003; Shelly et al. 2003, 2006a), survival rate (Shelly and McInnis 2003), and dispersal (Shelly and Edu 2008a).</li> </ul>
Ratio of protein to carbohydrates	<ul style="list-style-type: none"> <li>• Protein in dry diets early in adult life contributes to male sexual performance, but the ratio of protein to carbohydrates affects survival in a dose-dependent manner in <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, and <i>B. tryoni</i> (Prabhu et al. 2008; Gómez et al. 2013; Liedo et al. 2013; Liendo et al. 2013; Utgés et al. 2013).</li> <li>• As little as 4–10% of protein content in the pre-release diet is sufficient to significantly enhance male sexual performance in <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, and <i>B. tryoni</i> (Pérez-Staples et al. 2008a; Pereira et al. 2011; Gómez et al. 2013; Liedo et al. 2013; Liendo et al. 2013).</li> </ul>
Optimal formulation/delivery system	<ul style="list-style-type: none"> <li>• A formulation based on soy whey protein and incorporating methoprene has been developed and tested for <i>A. suspensa</i> (Teal et al. 2013).</li> <li>• Concurrently, a commercial product "Mubarqui" containing protein has been introduced in a dry formulation into release programmes for <i>A. ludens</i> and <i>A. obliqua</i> (Gómez and Teal 2010; Gómez et al. 2013).</li> </ul>
Dietary effects on remating inhibition	<ul style="list-style-type: none"> <li>• Feeding on a nitrogen-rich food significantly improves sterile male ability to inhibit female remating in <i>A. fraterculus</i> (Abraham et al. 2011, 2012, but see Abraham et al. 2013), <i>Bactrocera carambolae</i> Drew and Hancock, <i>B. tryoni</i>, <i>C. capitata</i>, and <i>Z. cucurbitae</i> (Pérez-Staples et al. 2008a; Gavriel et al. 2009; Haq et al. 2014a).</li> </ul>

Table 1. Continued

Subject addressed	Summary of results
Interaction between diet, dispersal, and survival	<ul style="list-style-type: none"> <li>• Protein-rich diets are related to a lower resistance to starvation in <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, <i>C. capitata</i>, and <i>B. tryoni</i> (Levy et al. 2005; Utgés et al. 2013; Reynolds et al. 2014; Juárez et al. 2019).</li> <li>• Adult diets that contain protein are related to lower recapture rates in protein-baited traps, and to reduced mobility and longevity in sterile <i>A. ludens</i>, <i>A. obliqua</i> (but not in <i>C. capitata</i>) males (Maor et al. 2004; San Andrés et al. 2009; Utgés et al. 2013).</li> <li>• Protein-rich post-teneral diets do not adversely affect the survival and movement in the field of sterile <i>B. tryoni</i> and <i>C. capitata</i> males (Yuval et al. 2007; Gavriel et al. 2010; Taylor et al. 2013b).</li> <li>• In the laboratory, protein-fed males live significantly longer than only sugar-fed males of <i>B. tryoni</i> and <i>Z. cucurbitae</i> (Haq et al. 2010b; Taylor et al. 2013b). The same was found for <i>A. ludens</i> and <i>A. obliqua</i> when the sugar:yeast ratio is 9:1 or 24:1, but not with a 3:1 ratio (Liedo et al. 2013).</li> <li>• In the laboratory, <i>B. tryoni</i> fed a 3:1 ratio of sugar:yeast for two days following emergence are more vulnerable to starvation if food is unavailable in the following days than if the flies are fed only sugar (Taylor et al. 2013a).</li> </ul>
Contribution of micro-organisms	<ul style="list-style-type: none"> <li>• Supplementing post-teneral diets with symbiotic bacteria reduces mass-rearing costs and increases mating success in fruit fly pests in SIT application (Cáceres et al. 2019; Noman et al. 2020; Raza et al. 2020; Augustinos et al., this volume).</li> <li>• The significant contribution of micro-organisms to the fitness of non-sterile <i>Bactrocera oleae</i> (Rossi) and <i>C. capitata</i> has been established (Behar et al. 2008a; Behar et al. 2005, 2008a, b, c; Ben-Ami et al. 2010; Gavriel et al. 2011; Hamden et al. 2013; Kyritsis et al. 2019). In <i>B. oleae</i>, the survival of males feeding on a probiotic diet is reduced compared with those fed on a sugar-only diet (Sacchetti et al. 2014).</li> <li>• Presence of commensal bacteria affect mate-selection behaviour of <i>B. dorsalis</i> (Damodaram et al. 2016).</li> <li>• Manipulating the microflora of sterile males by supplementing probiotic bacteria in adult diets can improve male sexual performance in <i>C. capitata</i> (Niyazi et al. 2004; Behar et al. 2005, 2008a, b, c; Ben-Ami et al. 2010; Gavriel et al. 2011; Hamden et al. 2013; Kyritsis et al. 2019), and in <i>A. obliqua</i>, <i>B. dorsalis</i>, and <i>Z. cucurbitae</i> (Rull et al. 2015; Yao et al. 2017; Cai et al. 2018; Stathopoulou et al. 2021).</li> </ul>
Irradiation effects mitigated by dietary supplements	<ul style="list-style-type: none"> <li>• Feeding with live bacteria can restore ecological fitness of males that were sterilized through irradiation in <i>B. dorsalis</i> (Cai et al. 2018).</li> <li>• Diet and irradiation affect micro-organism diversity in <i>B. tryoni</i> (Woruba et al. 2019).</li> <li>• Microflora diversity in laboratory-reared and irradiated males is low when compared with wild <i>C. capitata</i> males (Ben-Ami et al. 2010).</li> <li>• Irradiation significantly diminishes the ability of <i>B. tryoni</i> flies to tolerate protein deprivation (Pérez-Staples et al. 2007; Taylor et al. 2013b).</li> </ul>

Studies on the nutritional requirements of males of several tephritid species and their effect on sexual success (involving various species targeted by the SIT) have reached different levels of understanding. For example, studies in nature on *C. capitata* provide evidence that wild males feed on sources of protein (Hendrichs and Hendrichs 1990; Hendrichs et al. 1991). However, while providing yeast hydrolysates or other sources of protein together with sugar to males generally improved mating success in *Anastrepha*, *Bactrocera*, and *Zeugodacus* (Table 1), in *Ceratitidis* there is a variance in results reflecting the influence of other factors.

Different effects of protein-enriched diets have been found, in some cases reducing male survival and dispersal; the adverse effect was reduced when the protein ratio in the diet was lowered, but there are no clear procedural guidelines available currently for this and other target species (Blay and Yuval 1997; Shelly and Kennelly 2003; Shelly and McInnis 2003; Prabhu et al. 2008; FAO/IAEA 2017).

Moreover, there is evidence that the integrity of micro-organisms in the male gut contribute to fly health, foraging behaviour, and sexual performance (Yuval et al. 2013; Akami et al. 2019; Deutscher et al. 2019; Juárez et al. 2019; Augustinos et al., this volume). Adult diets enriched with different probiotic bacteria strains showed in irradiated *C. capitata* males a positive effect on the mating competitiveness, mating latency time, sexual calling or longevity (Niyazi et al. 2004; Behar et al. 2008b; Ben Ami et al. 2010; Gavriel et al. 2011).

Nevertheless, despite the increasing scientific evidence of the benefits of nutritional supplements, currently, possibly out of convenience, sterile males are often offered only a pre-release diet of highly concentrated sucrose, normally presented in an agar block, but without any protein addition. The formulation and testing of optimal pre-release diets, containing sugar, protein and probiotic bacteria (and possibly other ingredients) in proportions that will result in enhanced sterile male performance in the field, is still not fully understood and accepted by many operational programme managers, and remains to be implemented. However, the Moscamed programme in Mexico uses the Mubarqui adult diet for *C. capitata*, which contains proteins from diverse plant seeds (Gómez et al. 2013), and the Moscafrut programme in Mexico releases sterile *A. ludens* and *A. obliqua* flies fed with a 24:1 sugar:yeast adult diet. Managers should evaluate this matter in relation to their fruit fly species and decide on the most appropriate pre-release adult diet and feeding regime for sterile males.

### 3. HORMONAL TREATMENTS

Age is a significant factor affecting sexual signalling and reproduction in numerous tephritid species (Liedo et al. 2002; Pereira et al. 2013a). Being anautogenous, tephritid fruit fly pests in nature require a considerable period (over a week in *Ceratitis* spp.; 2–3 weeks in *Anastrepha* spp., *Bactrocera* spp., and *Zeugodacus* spp.) under adequate nutritional conditions to reach sexual maturation (Teal et al. 2013). Even though mass-rearing inadvertently selects for accelerated sexual maturation, the discrepancy between the standard holding periods at fly emergence and release facilities, and the time to reach sexual maturation, poses a significant problem for SIT programmes. After release but before reaching full sexual maturation, sterile males suffer significant losses due to predation and other causes, resulting in far fewer males surviving to maturity and copulation (Hendrichs and Hendrichs 1998; Rao et al. 2013; González-López et al. 2016).

Holding sterile males for more days also increases the management costs, and additional investment is required to expand the infrastructure at fly emergence and release facilities (USDA/APHIS 2009). In addition, in those programmes where sterile males are released together with sterile females, longer holding times are not advisable because males may start mating before release, thereby transferring their

limited sperm to sterile females. Clearly, the development of cost-effective methods to accelerate sexual maturity in released flies would have a significant positive impact on the efficacy of the SIT (Teal et al. 2000).

Research on several tropical *Anastrepha* species shows that juvenile hormone is a critical hormone, regulating sexual maturity and sexual signalling in these species (Table 2). Furthermore, application of juvenile hormone or the analogues, methoprene or fenoxycarb, can accelerate reproductive development and sexual signalling in sterile males of some species (Pereira et al. 2013a, b; Teal et al. 2013). Significant progress has been made in evaluating hormonal treatments using methoprene to accelerate reproductive development and, in some cases, improving further male sexual performance. It was found in many species (but not all) that sterile males become sexually mature significantly earlier when hormone exposure is included in pre-release holding protocols, but this optimum effect was only achieved when hormone treatment was coupled with a protein-enriched pre-release diet (Teal et al. 2013). Thus, irradiated males become sexually mature earlier and can be released earlier. This advantage is particularly important for SIT application against those species of *Anastrepha* spp., *Bactrocera* spp., and *Z. cucurbitae* that have long pre-copulatory periods. The improvement in male sexual performance by applying hormonal treatments was extensively studied in *Anastrepha* spp., *B. dorsalis*, *B. tryoni*, *Z. cucurbitae*, and *C. capitata*, although in these last two species no benefits were found. In addition, considerable progress was made in developing delivery systems to treat large numbers of flies with methoprene in operational programmes. The results on hormonal treatment assessments are described thematically in more detail, together with the relevant references, in Table 2.

Table 2. Summary of results, by thematic subject, of research conducted on the effects of pre-release application of hormonal treatments on male performance of tephritids of the genera *Anastrepha*, *Bactrocera*, *Ceratitis*, and *Zeugodacus* (modified after Pereira et al. 2013a, reproduced with permission)

Subject addressed	Summary of results
Age of sexual maturation of males determined	<ul style="list-style-type: none"> <li>• Age at which laboratory-reared and/or wild males of <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, <i>A. serpentina</i>, <i>A. striata</i>, <i>A. suspensa</i>, <i>B. correcta</i>, <i>B. dorsalis</i>, <i>B. tryoni</i>, <i>C. capitata</i>, <i>C. quilicii</i>, and <i>Z. cucurbitae</i> become sexually mature has been determined (Teal and Gómez-Simuta 2002; Aluja et al. 2009; Pereira et al. 2009; Gómez et al. 2013; Obra and Resilva 2013; Orankanok et al. 2013; Pereira et al. 2013b; Quilici et al. 2013; Segura et al. 2013; Sookar et al. 2013; Adnan 2019).</li> </ul>
Improvement in reproductive maturation and sexual performance	<ul style="list-style-type: none"> <li>• Hormonal treatment has positive effects on accelerating reproductive development and improving sexual performance in <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, <i>A. serpentina</i>, <i>A. striata</i>, <i>A. suspensa</i>, <i>B. tryoni</i>, and <i>Z. cucurbitae</i> (Aluja et al. 2009; Pereira et al. 2009; Segura et al. 2009; Haq et al. 2010a, 2013; Gómez et al. 2013; Collins et al. 2014; Gomez-Simuta et al. 2017; Bachmann et al. 2017; Adnan et al. 2020a).</li> <li>• In <i>A. fraterculus</i>, the accessory glands of males treated with methoprene are less effective at inhibiting female remating than males not treated with methoprene (Abraham et al. 2012).</li> <li>• There is no effect of hormonal treatment on either <i>B. dorsalis</i> or <i>C. capitata</i> (Faria et al. 2008; Shelly et al. 2009).</li> </ul>

Table 2. Continued

Subject addressed	Summary of results
Interaction of protein and hormone treatments on sexual performance	<ul style="list-style-type: none"> <li>• Males treated with hormone and feeding on a protein-rich diet effectively compete with mature wild males, but at significantly earlier ages for <i>A. fraterculus</i>, <i>A. ludens</i>, and <i>A. suspensa</i> (Gómez and Teal 2010; Liendo et al. 2013; Pereira et al. 2013b; Gómez et al. 2013).</li> <li>• Males of <i>Z. cucurbitae</i> treated with methoprene and with access to a protein-rich diet have an accelerated maturation and improved mating performance (Haq et al. 2010a).</li> </ul>
Interaction of irradiation and hormone treatments on sexual maturity	<ul style="list-style-type: none"> <li>• Interaction of irradiation and hormone treatments has no negative effects on male acceleration of reproductive maturity in <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, <i>A. suspensa</i>, and <i>B. tryoni</i> (Teal et al. 2007; Segura et al. 2013; Adnan et al. 2019).</li> <li>• Females mated with 6-day-old, methoprene-treated <i>A. fraterculus</i> males remated more and sooner than females mated with naturally matured males, either sterile or wild (Abraham et al. 2013).</li> </ul>
Optimal dose to accelerate maturation	<ul style="list-style-type: none"> <li>• Optimal hormone treatment dose has been determined using topical application for <i>A. fraterculus</i>, <i>A. ludens</i>, <i>A. obliqua</i>, <i>A. suspensa</i>, and <i>Z. cucurbitae</i> (Teal et al. 2007; Pereira et al. 2009; Segura et al. 2013; Haq et al. 2010a).</li> </ul>
Response in males and females to hormone treatments	<ul style="list-style-type: none"> <li>• A differential response in males and females to methoprene exposure is found in <i>A. fraterculus</i> and <i>B. tryoni</i>; it can act as a physiological sexing system, minimizing matings between sterile males and sterile females (Segura et al. 2009; Liendo et al. 2013; Adnan et al. 2019).</li> <li>• No differential response to methoprene exposure has been found in <i>A. ludens</i> males and females (Pereira et al. 2013b).</li> </ul>
Development of delivery systems other than topical application	<ul style="list-style-type: none"> <li>• Agar-based diet with 5–10% protein along with 0.05% methoprene, tested with <i>A. ludens</i> and <i>A. suspensa</i>, produces large amounts of waste and is not cost-effective (Pereira et al. 2013b; Teal et al. 2013).</li> <li>• Pupal dipping in an acetone bath containing 0.05% methoprene, tested with <i>A. fraterculus</i>, <i>A. ludens</i>, and <i>A. suspensa</i>, does not impact emergence or survival and accelerates reproductive development, although it can cause humidity problems when handling large volumes of pupae (Liendo et al. 2013; Pereira et al. 2013b; Segura et al. 2013).</li> <li>• Pupal dipping is impractical due to health risks, safety, and disposal issues associated with the use of acetone (Pereira et al. 2013a).</li> <li>• A dry sugar–protein pre-release diet containing 0.0015% methoprene for <i>A. ludens</i> and <i>A. obliqua</i> is practical and effective in accelerating development when applied in operations of fly emergence and release facilities (Gómez et al. 2013).</li> <li>• Dietary treatment with mosquito larvicide containing methoprene in a dry 3:1 mix of sugar to yeast is effective in <i>B. tryoni</i> (Adnan 2019; Adnan et al. 2019, 2020a).</li> </ul>
Efficient large-scale methods for incorporation of JH analogues	<ul style="list-style-type: none"> <li>• The dry sugar–protein–methoprene diet method was assessed in a 3500-ha pilot area for <i>A. ludens</i> in Mexico (Gómez et al. 2013).</li> <li>• The hormone and protein delivery system has tested positive in the “Moscafrut” action programme to control <i>A. ludens</i> fruit flies in Mexico (Gómez et al. 2013).</li> </ul>



#### 4. SEMIOCHEMICAL TREATMENTS

Males of most *Anastrepha* spp., *Bactrocera* spp., *Ceratitis* spp., and *Zeugodacus* spp. are attracted to natural compounds known as semiochemicals (Cunningham 1989; Kumaran et al. 2013; Segura et al. 2018). Some species are known to sequester these chemicals from plants for use in pheromone synthesis; for example, ingestion of methyl eugenol (ME) from natural sources by males of *B. dorsalis* and *B. carambolae* results in the storage of metabolites in the rectal gland and their subsequent release as part of the pheromone during fanning performed in courtship (Tan and Nishida 1996). Providing sterile *B. dorsalis* males with a source of ME to feed on before release could increase their mating competitiveness (Shelly et al. 2005). ME feeding may also confer a survival advantage because metabolites appear to act as a very potent allomone to deter vertebrate predators (Wee and Tan 2001).

In the case of *C. capitata*, exposure to ginger (*Zingiber officinale* Roscoe) root oil (GRO) or citrus oils (by contact or vapour) enhances considerably the mating competitiveness of wild or mass-reared males (Katsoyannos et al. 1997; Papadopoulos et al. 2001; Shelly 2001).

Exposure to guava (*Psidium guajava* L.) fruit volatiles increased the mating success of both wild and laboratory *A. fraterculus* males relative to non-exposed males (Vera et al. 2013). Also, citrus and grapefruit volatiles have potential to enhance the mating performance of male *A. ludens* and *A. fraterculus* (Bachmann et al. 2015; Morató et al. 2015). However, the attraction and mating enhancing effects of the semiochemicals so far found for *Anastrepha* effects are not as dramatic as seen with *Bactrocera*, *Ceratitis* and *Zeugodacus*, and suggest that similar compounds may exist in the *Anastrepha* ecological sphere and await discovery (Segura et al. 2018).

The research carried out in this area has helped to understand these phenomena, to extend them to other species, and to transfer and validate them under the large-scale conditions of action SIT programmes. Results obtained recently confirmed the compounds that have the potential to improve sterile male performance of target fruit flies in the field, and some additional ones have been identified. These chemicals are the following:

- Methyl eugenol (ME) is found in more than 450 plant species (Tan and Nishida 2012); exposure to holy basil (*Ocimum tenuiflorum* L.) and sweet basil (*Ocimum basilicum* L.) oils, as well as ripe fruits of tropical almond (*Terminalia catappa* L.), improve the mating competitiveness of several *Bactrocera* species, including *B. correcta*, *B. dorsalis*, and *B. zonata* males (Cunningham 1989; Tan and Nishida 1996; Quilici et al. 2004; Shelly et al. 2005; Shelly and Edu 2007; Obra and Resilva 2013; Orankanok et al. 2013).
- Cuelure (CUE) has potential to enhance the performance of *B. tryoni* and *Z. cucurbitae* males (Weldon et al. 2008; Shelly 2019).
- Raspberry ketone (RK) and/or zingerone (ZG) have potential to enhance attraction, maturation, and sexual performance of *B. tryoni* and *Z. cucurbitae* males (Khoo and Tan 2000; Akter et al. 2017b; Akter and Taylor 2018; Shelly 2019); however, Fezza and Shelly (2018) did not find that access to a RK-supplemented diet at an early age accelerated sexual maturation.

- Ginger root oil (GRO) and  $\alpha$ -copaene enhance male performance of *C. capitata* and *C. quilicii* (Shelly 2001; Shelly et al. 2007a; Quilici et al. 2013).
- Manuka oil (rich in  $\alpha$ -copaene) from the manuka tree (*Leptospermum scoparium* Forst and Forst) of New Zealand improves *C. capitata* male mating (Shelly et al. 2008c).
- Orange oils (OO) and other citrus oils enhance male performance of *C. capitata* and *C. quilicii*, and potentially *A. fraterculus* (Shelly 2001; Shelly et al. 2007a; Quilici et al. 2013; Vera et al. 2013).
- Citrus, grapefruit, and guava fruit volatiles have potential to enhance the mating performance of male *A. ludens* and *A. fraterculus* (Vera et al. 2013; Bachmann et al. 2015; Morató et al. 2015).

The results of assessing semiochemical treatments, together with the relevant references, are described in more detail in Table 3.

Methodologies for exposing large numbers of *C. capitata* males through GRO or citrus-oil aromatherapy on a large scale in adult-holding rooms at fly emergence and release facilities have been developed (Shelly et al. 2007c, 2008a). They are now applied routinely in a very cost-effective manner in on-going SIT programmes in Australia, Croatia, Guatemala, Israel, Mexico, Spain, and the USA, resulting in a significant improvement in mating performance of the released sterile males.

It is envisaged that providing sterile *Bactrocera* spp. males with a source of ME to feed on before release will place them on at least an even “playing field” against wild males, thereby potentially reducing the number or frequency of sterile males released (Barclay et al. 2014; Vargas et al. 2014). However, the common methods for holding sterile males in fly emergence and release facilities do not enable the feeding of ME to millions of adult flies after their emergence. Additionally, exposure to ME must be brief in view of ME toxicity when access is unlimited. In response, Tan and Tan (2013) designed an automated ME machine prototype for briefly feeding ME to sterile males on a belt impregnated with ME after which they are brushed off and collected. However, this approach is not really suitable for industrial processing of millions of sterile males. Considering this scenario at fly emergence and release facilities, Haq et al. (2014b, 2015, 2018) demonstrated that ME application by aromatherapy also enhanced the mating success of males of *B. carambolae* and *B. dorsalis*, finding that ME aromatherapy produced a mating boost as early as one day after exposure. This alternative method appears to have merit for adoption but needs to be evaluated at larger scales in fly emergence and release facilities.

Another advantage of exposure to ME is that it reduces significantly the response of sterile males to ME in male annihilation treatments, thus potentially enabling the simultaneous application of the SIT and male annihilation (Barclay et al. 2014; Vargas et al. 2014). Similarly, pre-release exposure to RK has been found to diminish the subsequent response of *B. tryoni* to CUE sources (Akter et al. 2017a).

Table 3. Summary of results, by thematic subject, of research conducted on the effects of pre-release application of semiochemical treatments on male performance of tephritids of the genera *Anastrepha*, *Bactrocera*, *Ceratitis*, and *Zeugodacus*. Abbreviations explained in the text (modified after Pereira et al. 2013a, reproduced with permission)

Subject addressed	Summary of results
Search for semiochemical compounds that affect <i>Anastrepha</i> spp. male sexual performance	<ul style="list-style-type: none"> <li>• Grapefruit volatiles increase male mating competitiveness in <i>A. ludens</i> (Morató et al. 2015).</li> <li>• Male mating performance of <i>A. fraterculus</i> is positively affected by exposure to guava volatiles (Vera et al. 2013; Bachmann et al. 2015).</li> <li>• Exposure to lemon fruit volatiles enhances male mating performance in <i>A. fraterculus</i>, but there are also some detrimental effects (Vera et al. 2013). GRO exposure also increases male mating success in <i>A. serpentina</i> (Flores et al. 2011).</li> </ul>
Assessment of various semiochemicals in enhancing <i>Bactrocera</i> spp. male performance	<ul style="list-style-type: none"> <li>• Exposure to basil oil (containing ME) has a positive effect on sterile male mating performance of <i>B. dorsalis</i> (Obra and Resilva 2013).</li> <li>• Exposure to ripened tropical almond fruit (containing ME) enhances <i>B. dorsalis</i> male mating success (Shelly and Edu 2007).</li> <li>• Exposure to ME significantly improves sterile male mating performance of <i>B. correcta</i> and <i>B. dorsalis</i> (Shelly et al. 1996, 2005, 2008b, 2009, 2010a; Hee and Tan 1998; Shelly and Edu 2008b; Ji et al. 2013; Orankanok et al. 2013).</li> <li>• Some negative effects on the male ejaculate have been found in <i>B. dorsalis</i> (Reyes-Hernández et al. 2019).</li> <li>• ME-mediated male mating enhancement also found in <i>Bactrocera cacuminata</i> (Hering) (Raghu and Clarke 2003), <i>B. carambolae</i> (Wee et al. 2007), and <i>Bactrocera umbrosa</i> (F.) (Wee et al. 2018).</li> <li>• Exposure to commercial ME, and interaction with post-teneral adult diet, increases male mating performance of <i>B. correcta</i> and <i>B. dorsalis</i>. For both species, ME-treated sterile males are being released in operational SIT programmes in Thailand (Orankanok et al. 2013).</li> <li>• Sterile males, feeding on commercial ME prior to release, induce higher egg sterility in wild populations than control sterile males denied ME (McInnis et al. 2011).</li> <li>• Exposure to ME does not affect dispersal or survival of sterile flies of <i>B. correcta</i> and <i>B. dorsalis</i> (Orankanok et al. 2013).</li> </ul>
Assessment of various semiochemicals in enhancing male performance of other <i>Bactrocera</i> spp.	<ul style="list-style-type: none"> <li>• Feeding on CUE increases <i>Z. cucurbitae</i> mating success (Shelly and Nishimoto 2017). Feeding on RK enhances male mating performance of <i>Z. cucurbitae</i>, but only for one day post-feeding (Shelly 2000, 2019). However, exposure to zingerone has no effect on <i>Z. cucurbitae</i> male mating competitiveness (Shelly 2017b) or a positive effect only one day after exposure (Inskeep et al. 2019).</li> <li>• Exposure to CUE and RK increases the mating competitiveness of <i>B. tryoni</i>, but young males fail to respond to CUE, OO, and GRO (Weldon et al. 2008; Kumaran et al. 2014a; Akter et al. 2017b).</li> <li>• <i>B. tryoni</i> feeding on yeast hydrolysate enhances attraction to CUE (Weldon et al. 2008), and on CUE increases male signalling, female attraction, and male mating success (Kumaran et al. 2013, 2014b).</li> <li>• <i>B. tryoni</i> feeding on RK (or caffeine supplements) promotes male early sexual maturation, greater mating success and increased multiple mating, without affecting remating receptivity in females (Akter et al. 2017b; Akter and Taylor 2018; Khan et al. 2019; Adnan et al. 2020b; GFV 2020).</li> <li>• Exposing sexually mature adult <i>B. oleae</i> to the aroma of <math>\alpha</math>-pinene significantly increases the mating performance over non-exposed males and females (Gerofotis et al. 2013; Kokkari et al. 2017).</li> </ul>

Table 3. Continued

Subject addressed	Summary of results
Optimal age and feeding dose for <i>Bactrocera</i> spp. male flies	<ul style="list-style-type: none"> <li>• For <i>B. dorsalis</i>, Obara and Resilva (2013) determined the optimal age and duration of ME exposure, and the diurnal pattern of ME feeding.</li> <li>• Optimal age of ME exposure, in combination with nutritional supplements, has been determined for sterile <i>B. correcta</i> and <i>B. dorsalis</i> males (Orankanok et al. 2013).</li> </ul>
Effect of semiochemical treatments on <i>C. capitata</i> sexual signalling (pheromone calling)	<ul style="list-style-type: none"> <li>• GRO-exposed males exhibit higher rates of sexual signalling compared with unexposed <i>C. capitata</i> males (Shelly 2001, 2007a, 2008, 2010b; Papadopoulos et al. 2006), although the effect found by Briceño et al. (2007) was lower.</li> <li>• During sexual courtship GRO-exposed sterile males exhibit the same wing-beat duration as wild males, and this is shorter than for unexposed sterile males (Morelli et al. 2013).</li> <li>• Exposure to OO and their components increases sexual signalling and mating success of <i>C. capitata</i> males (Shelly et al. 2004, 2006b; Kouloussis et al. 2013); this effect is more pronounced in protein-fed males, independent of age (Katsoyannos et al. 2004; Papadopoulos et al. 2006; Kouloussis et al. 2013, 2017).</li> <li>• Exposure to volatiles of leaves of the tea tree increases mating competitiveness of sterile <i>C. capitata</i> males (Shelly and Epsky 2015).</li> </ul>
Identification of active compounds other than GRO, and their effects on sexual performance of <i>C. capitata</i>	<ul style="list-style-type: none"> <li>• Exposure to oranges and grapefruits (<i>Citrus paradisi</i> Macfad) improves mating success of male <i>C. capitata</i> (Papadopoulos et al. 2001; Shelly 2009).</li> <li>• Exposure to fruits of five citrus species shows that sweet oranges confer the highest increase in male mating performance of <i>C. capitata</i>. Exposure to commercial citrus oils is similarly effective (Kouloussis et al. 2013).</li> <li>• There is a positive effect of OO components (limonene, <math>\beta</math>-myrcene, and linalool) on protein/sugar-feeding males, but not on sugar-only-feeding males (Kouloussis et al. 2013).</li> <li>• A mixture of limonene, <math>\beta</math>-myrcene, linalool, <math>\alpha</math>-pinene, and geraniol (1:1:1:1:1) is very effective for both wild and sterile <i>C. capitata</i> male sexual performance (Kouloussis et al. 2013).</li> </ul>
Effects of GRO and OO exposure to <i>C. quilicii</i>	<ul style="list-style-type: none"> <li>• Exposure of sugar-only-fed <i>C. quilicii</i> males to GRO and OO increases their mating performance, but only GRO increases the mating performance of protein/sugar-fed males (Quilici et al. 2013).</li> </ul>
Effect of semiochemical treatments on <i>C. capitata</i> female remating frequency	<ul style="list-style-type: none"> <li>• The remating frequency of <i>C. capitata</i> females mated with sterile males treated with 0.1 ml/m<sup>3</sup> GRO is similar to that of females mated with wild males and lower than that of females mated with sterile unexposed males (Morelli et al. 2013).</li> </ul>
Effect of semiochemical treatments on <i>C. capitata</i> dispersal and survival	<ul style="list-style-type: none"> <li>• Field dispersal and survival rates of GRO-exposed sterile males are similar to those of unexposed <i>C. capitata</i> males (San Andrés et al. 2009; Paranhos et al. 2010; Juan-Blasco et al. 2013).</li> </ul>
Determining the dose of semiochemical exposure for <i>C. capitata</i>	<ul style="list-style-type: none"> <li>• OO compounds show positive effects in increasing <i>C. capitata</i> male performance (Kouloussis et al. 2013). The optimal dose of OO exposure was determined for both protein-sugar and sugar-only <i>C. capitata</i> adult diets. There are positive effects of OO for a protein-sugar diet, but no effects for a sugar-only diet (Kouloussis et al. 2013).</li> </ul>
Optimal delivery system for large-scale semiochemical application in <i>Ceratitidis</i> spp. SIT programmes	<ul style="list-style-type: none"> <li>• The cost-effective GRO exposure to sterile males has been established, and is in operation in several <i>C. capitata</i> SIT programmes (Shelly et al. 2007b, c, 2008a; Paranhos et al. 2008, 2013; Juan-Blasco et al. 2013; Silva et al. 2013; Steiner et al. 2013).</li> </ul>

## 5. CONCLUSIONS

Extensive laboratory and semi-field tests indicate that pre-release diets nutritionally enriched with some yeast hydrolysate improve sterile male performance; they can result in increased SIT efficiency for a majority of fruit fly species tested, and thus can be adopted by programme managers, although some confounding factors still need to be better understood for some target species, as well as the optimal protein to carbohydrate ratios and physical form of diet provision. Also, a better understanding of the effect of nutrition during the larval stage on the nutritional requirements of the adults is needed (Aluja et al. 2009).

In addition, hormone therapy coupled with feeding protein to adults generally accelerates male maturation and sexual performance among *Anastrepha* species and some *Bactrocera* species, with no negative side effects on survival. Furthermore, in some species, methoprene treatment has increased male mating and competitiveness. However, negative effects have been recorded on female remating in *A. fraterculus*, and on sperm storage and male ejaculate in *B. dorsalis*.

Accelerated male maturation and improved sexual performance can represent significant cost savings associated with infrastructure investment, reduced holding periods for sterile males prior to release, and fewer males dying in the field before reaching sexual maturity. Validation in a few fruit fly species has resulted in some of these major breakthroughs being incorporated into several action programmes, although others, for technical or practical reasons, have been reluctant to incorporate these innovations into their operations.

The development of cost-effective semiochemical treatments that improve sterile male sexual signalling and attractiveness to wild females, and thus overall mating performance, is highly desirable. Implementation of aromatherapy has significantly increased the effectiveness of on-going programmes integrating the SIT against *C. capitata*. On the other hand, while the incorporation of semiochemical treatments for *Bactrocera* species appears to be feasible, it still remains to be implemented operationally; major benefits result from the simultaneous field application of male annihilation to eliminate wild males. Thus, incorporating an ME pre-release treatment has considerable potential to significantly increase sterile to wild male overflooding ratios (Barclay et al. 2014; Vargas et al. 2014; Hendrichs and Robinson, this volume). For some *Anastrepha* species and other species such as *B. oleae* and *C. quilibicci*, potentially similar semiochemicals and fruit volatiles probably exist, and more research funding should be allocated to find and investigate them (Segura et al. 2018).

Also critical for sterile male performance are the processes to which sterile males are subjected at fly emergence and release facilities (USDA/APHIS 2009; FAO/IAEA 2017; Dowell et al., this volume), the environmental conditions in which they are held, and their interaction with exposure to hormonal, nutritional and/or semiochemical treatments (Pereira et al. 2013a). In addition, holding densities (Diaz-Fleischer et al. 2009; Andress et al. 2015), the timing of providing treatments in relation to fly age and sexual maturation, and holding periods are also very relevant. For example, results indicate that in *C. capitata* sexing strains, the release of older males, closer to sexual maturity, is preferable; this results in more flies reaching mating age in the field (McInnis et al. 2013). Species with longer pre-copulatory

maturation periods, such as *Anastrepha* spp. and *Bactrocera* spp., benefit more from combined nutritional and hormonal treatments to reduce long pre-release holding periods (Gómez et al. 2013; Pereira et al. 2013a).

Assessing the interaction of different environmental and holding conditions, combined with hormonal, nutritional, and/or semiochemical treatments, on sterile fly performance has resulted in the routine application of GRO under large-scale holding conditions in operational *C. capitata* SIT programmes (USDA/APHIS 2009; FAO/IAEA 2017). Also, a hormone-and-protein-delivery system has been developed for the SIT programmes suppressing *A. ludens* fruit fly populations in Mexico (Gómez et al. 2013). Furthermore, the effects on fly performance (in terms of dispersal and recapture) of different sterile fly shipping and release systems, and their interaction with hormonal, nutritional, and/or semiochemical treatments, have been assessed for some aerial- and ground-release systems for *C. capitata* (Paranhos et al. 2010, 2013; Silva et al. 2013). Finally, parameters of sterile-fly quality, treatments, space, labour, and economics were assessed and compared at eight fly emergence and release facilities in Guatemala, Mexico, and the USA (USDA/APHIS 2009); there is a good baseline on which to improve.

Knowledge gained so far, and the practical procedures developed, are transferable, at least in part, to other insect pest species with management programmes that include an SIT component. Nevertheless, much remains unknown about the effects of manipulating the environmental holding conditions, either separately or in combination with nutritional, hormonal, and semiochemical treatments, on subsequent male quality in the field. Release methods, while operationally convenient, are not always optimal in terms of sterile male performance (Dowell et al., this volume). For example, the effect of chilling (to immobilize) collected flies for aerial release can at least temporarily affect sterile male flight ability and mating competitiveness, including pheromone quantity or quality (Andress et al. 2012, 2013; Shelly et al. 2013; Arredondo et al. 2016). Therefore, the effects and interactions of the different processes, treatments, and systems need to be further assessed and refined, tailoring them to the biology of each target fruit fly species.

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