CHAPTER 1.2.

MISCONCEPTIONS AND CONSTRAINTS DRIVING OPPORTUNITIES

M. WHITTEN¹ AND R. MAHON²

¹*The University of Queensland, Brisbane, Queensland 4072, Australia*

Email: max_w@aapt.net.au

²*CSIRO Entomology, Canberra ACT 2601, Australia*

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V. A. Dyck, J. Hendrichs and A. S. Robinson (eds.), Sterile Insect Technique. Principles and Practice in Area-Wide Integrated Pest Management. Second Edition.

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SUMMARY

In theory, the sterile insect technique (SIT) is applicable to a wide variety of invertebrate pests. However, in practice, the approach has been applied successfully to only a few major pests. Chapters in this volume address possible reasons for this discrepancy, e.g. Klassen et al., Lance and McInnis, and Hendrichs and Robinson. The shortfall between theory and practice is partly due to the persistence of some common misconceptions, but it is mainly due to one constraint, or a combination of constraints, that are biological, financial, social or political in nature. This chapter's goal is to dispel some major misconceptions, and view the constraints as challenges to overcome, seeing them as opportunities to exploit. Some of the common misconceptions include: (1) released insects retain residual radiation, (2) females must be monogamous, (3) released males must be fully sterile, (4) eradication is the only goal, (5) the SIT is too sophisticated for developing countries, and (6) the SIT is not a component of an area-wide integrated pest management (AW-IPM) strategy. The more obvious constraints are the perceived high costs of the SIT, and the low competitiveness of released sterile males. The perceived high up-front costs of the SIT, their visibility, and the limited private investment (compared with alternative suppression measures) emerge as serious constraints. Area-wide SIT application is management intensive, requiring effective and dedicated management; insufficiently trained, funded or committed managers can negatively affect successful implementation. Failure to appreciate the true nature of genetic approaches, such as the SIT, may pose a significant constraint to the wider adoption of the SIT and other genetically-based methods, e.g. transgenic genetically modified organisms (GMOs). Limited support for the necessary underpinning strategic research also appears to be an important constraint. Hence the case for extensive strategic research in ecology, population dynamics, genetics, and insect behaviour and nutrition is a compelling one. Raising the competitiveness of released sterile males remains the major research objective of the SIT.

1. INTRODUCTION: CHALLENGE OF A NOVEL METHOD FOR AREA-WIDE INTEGRATED PEST MANAGEMENT

The 20th century witnessed at least four major advances in methods of suppressing pestiferous invertebrates. The two most ubiquitous of these, synthetic pesticides and biological control, did not require any prior conceptual revolution in scientific thinking for their development and adoption. Both approaches witnessed significant technical innovations, but, conceptually, each was essentially "more of the same". In contrast, the other two important approaches to pest management, autocidal/genetic control (including the sterile insect technique (SIT)) and, more recently, genetically modified organisms (GMOs), have emerged from a totally new worldview as to how each generation passes on the "instructions of life". No language could even come close to explaining these genetic approaches before the 20th century and the influence of Darwin and Mendel. They were simply beyond anticipation (Whitten 1985).

The existence of DNA, and just how these giant molecules might carry the heredity blueprints from one generation to the next as cryptic coded information, was completely outside the thinking of 19th century scientists. Advances in the discipline of genetics — the study of change during an individual's development, and variation between populations over space and time — became the hallmarks of 20th century biology. Not surprisingly, genetics and evolutionary concepts now impinge on many aspects of pest management. They shape our understanding of pesticide resistance and its management (McKenzie 1996), help us determine the specificity and safety of biocontrol agents (Whitten and Hoy 2000), and facilitate the design of novel genetic tactics for pest suppression such as the SIT (Knipling 1955, 1979) and chromosomal rearrangements (Serebrovskii 1940; Curtis 1985; Whitten 1985). They have also enabled researchers to identify toxin-producing, pesticide- and disease-resistant, and

other relevant genes, along with the means to transfer such information to unrelated species, whether crop plants or insects (Häcker et al., this volume).

Unlike biological control or pesticides, both household concepts, an important corollary of the genetics revolution has been a need for the broader community to understand the nature of the hereditary material, and how we can manipulate it, to appreciate the risks and benefits of genetics-based approaches to pest control. Even then, some understanding of ecology and economics is required to put the basket of tactics into a realistic context. In comparison with other pest control tactics, it is difficult for stakeholders, without a basic level of knowledge, to make informed decisions about whether to support or oppose the SIT and transgenic GMOs. Herein lies the biggest constraint to the successful application of the SIT and other genetic means of pest suppression.

It is important that scientists and their institutions enter into meaningful dialogue with the ultimate beneficiaries of genetic approaches to pest control, particularly farmers and communities affected by insect pests and insect-borne diseases, but also the wider public. This is especially true in developing country-generated initiatives; and formal requests for area-wide integrated pest management (AW-IPM) programmes that integrate the SIT are often unrealistic, their implementation is poorly managed (including corruption in some cases), and they lack close interaction with local communities and other stakeholders (Dyck, Regidor Fernández et al., this volume; Dyck, Reyes Flores et al., this volume) (Box 1).

Box 1. Unsuccessful Attempts to Deploy the SIT and Genetic Control of Mosquito-Borne Disease Vectors in India

The value of achieving a joint understanding and ownership of genetic control tactics can be illustrated by reference to the unsuccessful attempts of the World Health Organization (WHO) and the Indian Council of Medical Research (ICMR) to develop novel genetic control tactics for three mosquito vectors of disease (malaria, yellow fever and filariasis) in rural India during the 1970s. This ambitious programme evaluated three approaches to genetic control, namely the SIT using either irradiation or chemosterilants, and chromosomal rearrangements (Davidson 1974). Initially, some common ground for this pioneering project was created when the general approach was described to rural communities as family planning for mosquitoes — a concept widely promoted for human population control by the Indira Ghandi Government. Unfortunately, the mosquito programme floundered when journalists, exploiting ignorance and prejudice, persuaded Indian politicians that the project was designed to serve foreign interests and not the national well-being. The programme was abruptly abandoned in 1975, to the chagrin and embarrassment of the WHO and ICMR, to the bewilderment of many, and, undoubtedly, to the lasting detriment for rural communities scourged by mosquito-borne diseases (Nature 1975; WHO 1976; Dyck, Regidor Fernández et al., this volume). There may be some parallels between the attempts for genetic control of mosquito populations in India and those for the eradication of some tsetse *Glossina* populations in Africa. These include the risks of using foreign aid to implement sophisticated technologies not adequately understood by the intended beneficiaries, with the expectation of eliminating a suite of disease vectors on a large area-wide basis covering different political entities and diverse ecologies.

A study on the efficacy, economics and social impact of genetically engineered *Bt*-cotton in China illustrates well the importance of technology users having a reasonable understanding of the available pest control tactics (Pemsl et al. 2003). A similar conclusion can be drawn about the evolution of resistance and its management, whether we are talking about pesticides, GMOs, or the SIT. Not surprisingly, in very few countries is the concept of resistance management understood and effectively

applied (McKenzie 1996). Without doubt, a major challenge for proponents of genetic-based interventions is to secure from participating countries, their communities (especially in rural areas), and relevant stakeholders the prior informed consent, commitment and genuine ownership of the proposed programme (Dyck, Reyes Flores et al., this volume). Otherwise, misconceptions will arise, and serious constraints can emerge unnecessarily.

Finally, a brief case study of tsetse suppression/eradication in Africa illustrates how misconception and constraint can interplay to influence decision-makers on the feasibility of pest control options surrounding the SIT. Ironically, tsetse fly suppression/eradication, using sterile hybrids (Vanderplank 1947), is often cited as the first convincing field demonstration of autocidal control of an insect pest (Krafsur 1998; Klassen et al., this volume; Robinson, this volume). Yet, subsequent attempts at area-wide eradication of tsetse populations, first with chemicals, and then integrating the SIT, have achieved some success (Vreysen et al. 2000), but have also attracted controversy (Linear 1985; Rogers and Randolph 2002). For example, it is claimed that the pesticide campaign of the Food and Agriculture Organization of the United Nations (FAO), costing about USD 1000 million by 1985, increased rather than reduced the distribution of tsetse (Linear 1985). Important ecological aspects of the debate, such as the role of tsetse in “protecting” vast tracts of natural habitat from occupation by human populations with environmentally damaging cattle ranching, are not directly germane to this discussion. Nevertheless, Nagel and Peveling (this volume) state that new areas are opened up to cultivation as a result of rapidly increasing human population pressure in sub-Saharan Africa, independent of tsetse presence or absence. However, other criticisms levelled by Linear, and partly revived more recently (Rogers and Randolph 2002), at SIT-based tsetse programmes, are more pertinent (Box 2).

2. SOME COMMON MISCONCEPTIONS

2.1. *Are Irradiated Insects Radioactive?*

During the early development of the SIT, chemosterilants were assessed but abandoned, mainly because of concern over the release of sterile insects with residues of non-specific chemosterilants into the environment (Lance and McInnis, this volume; Robinson, this volume). All current and proposed programmes that release sterile insects use Co-60, Cs-137, or X-rays as the irradiation source (Bakri et al., this volume). Is there a similar risk that irradiated insects contain harmful residual radiation?

A study of the irradiation of foodstuffs, where irradiation levels are much higher, dispels this fear. The conclusion of all the studies on irradiated foods for human or animal consumption indicates that there are no levels of residual radiation to give cause for concern. The issue of greater concern was related to the production of biologically active compounds that could be harmful. Again, this concern has been dismissed as insignificant.

Is irradiated food radioactive? The process of irradiating food is regulated and designed to ensure that that is not the case. The radiation sources used to irradiate food

and agricultural products (including insects) are restricted to: gamma rays from the radionuclides Co-60 and Cs-137, and accelerator-generated radiation either as 10 million electron volt (MeV) electrons or 5 MeV X-rays (FAO 2003). Also, it is important to realize that food (non-irradiated), and any natural substance, contain natural radioactivity that can be measurable. Therefore, it is important to put in perspective the issue of possible induced radioactivity in food and natural radioactivity in food. In a document published by the IAEA (2002a), all relevant data generated over the last 40–50 years, and various nuclear mechanisms that can produce radioactivity, were analysed, and it was concluded that:

... the increase in radiation background dose from consumption of food irradiated to an average dose below 60 kGy with gamma rays from Co-60 or Cs-137, with 10 MeV electrons, or with X-rays produced by electron beams, with energy below 5 MeV, is insignificant. It is best characterized as zero.

Box 2. Can Tsetse Species be Suppressed/Eradicated by the SIT?

The debate on the potential of the SIT to suppress/eradicate large tsetse populations indicates a mix of misconceptions, and possibly some significant constraints. These include:

- The SIT is highly technological (a misconception driven by inadequate understanding, but to the extent that this is true, the quality of its implementation, which is essential for successful SIT application, can be negatively affected by insufficiently trained or paid managers).
- At least 31 species and subspecies of *Glossina* are disease vectors, with various mating barriers between taxa. (In fact, most tsetse taxa are not economically important, and are restricted to rain forests, having little contact with humans or domestic animals. In Kenya, for example, elimination of populations of *G. pallidipes* Austen would eliminate the entire agricultural problem. In Ethiopia, two species are important — *G. pallidipes* and *G. morsitans* ssp.).
- The complexity and difficulty of the problem — with 10 million km², more than 30 countries infested, and multiple taxa — pose immense logistical, financial and coordination problems, especially if eradication is the objective. In fact, only selected populations in priority areas at the edge of tsetse belts are currently being targeted (Feldmann et al., this volume).
- The possibility exists that a neighbouring non-target tsetse species would invade an empty niche following the application of the SIT. This could apply to *G. pallidipes* and *G. morsitans*, which are sometimes sympatric.
- Expensive pre-release field studies are required to determine species presence, distribution and abundance (part misconception, and probably an overstated constraint).
- Target tsetse populations are often remote from human population centres (a logistical challenge?).
- Multiple-mating of females, thereby possibly reducing the effective impact of sterile males, is largely a misconception (section 2.3.).
- Sterile tsetse males can act as disease vectors, and the argument of “net benefits” may not suffice (in fact, steps are routinely taken to prevent males from acting as disease vectors (Feldmann et al., this volume; Nagel and Peveling, this volume).
- Pre-release tsetse population reduction measures, e.g. pesticides and trapping, are required (integration with other pest management approaches could be seen as a strength).
- The SIT can be prohibitively slow and costly, and large up-front costs presupposing eradication represent a constraint. However, the low economic returns from animal traction, livestock production and other benefits resulting from eradication are a misconception as shown by the major benefits deriving from the eradication of *Glossina austeni* Newstead from the island of Unguja in Zanzibar (Feldmann et al., this volume).
- Failure to eradicate could represent a zero return on a substantial investment, although temporary suppression is also the goal of other tactics.
- Technological complexities and poor economics create difficulties in obtaining sponsorship (a constraint).

In recent years the use of irradiation for protecting foodstuffs to meet quarantine and sanitation requirements has become more mainstream without adverse incident (Heather and Hallman 2008). For example, for years all guava exported from Mexico to the USA is irradiated (The Packer 2011), and honeybee hives, infected with bacterial diseases or arthropod pests, are routinely commercially decontaminated with gamma radiation, reducing the need to destroy valuable equipment (Titěra 2009; Queensland Government 2018).

The above facts about food irradiation and related applications can be extended to insect sterilization procedures, since the same sources of irradiation are used (Co-60, Cs-137, electrons or X-rays). Furthermore, insect sterilization for sterile insect releases requires a much lower radiation dose than for food irradiation. In food irradiation, the dose varies from about 100 Gy to 60 kGy, depending on the end objectives. In insect sterilization, the dose is in the range of only 100–300 Gy, depending on the insect and irradiation conditions (Hallman 2000; Bakri et al. 2005; IDIDAS 2018; Bakri et al., this volume). Thus, the induction of radioactivity in insects irradiated for programmes that release sterile insects can also be “best characterized as zero” (Elias and Cohen 1977; Terry and McColl 1992; IAEA 2002a, b).

Given the low levels of irradiation given to insects, the small biomass of the released insects and their wide dispersal, there are no plausible grounds for concern about residual radioactivity, or radiation-induced toxins, in released insects. Conversely, one might argue that the SIT is more environment-friendly than some alternative suppression tactics such as synthetic pesticides or augmentative or classical biological control. Pesticide contamination of foodstuffs, exposure and poisoning of workers, and environmental damage are often very real issues, particularly in developing countries (EJF 2002, 2003). The absence of any collateral damage following directly from the release of radiation-sterilized insects into the environment is indeed one of the strengths of the SIT, compared with chemical control, biocontrol or even GMOs. As with GMOs, concern about the process, and not the product itself, is sometimes the basis for apprehension. It would be very unfortunate if this misconception about the SIT ever became the reason for an otherwise viable AW-IPM programme not being implemented.

2.2. In What Sense Are “Sterile Insects” Sterile? Is This a Misnomer or a Misconception?

In terms of physiology and behaviour, male insects “sterilized” by gamma radiation are not sterile (Robinson, this volume). Indeed, they are expected to generate viable and functional sperm capable of fertilization, to produce a full complement of seminal fluids, and also to enjoy undiminished libido. The population-suppressing impact of released sterile males is realized via radiation-induced dominant lethals that are lethal in the next or subsequent generations. By way of contrast, irradiated females may produce fewer or no eggs, and their behaviour may well differ in other critical ways from normal non-irradiated females. Thus “conventional” sterility is often induced in females, but that is of no consequence in many programmes that release only sterile males.

In species where females multiple-mate and store sperm in spermathecae, it is important that irradiated sperm from sterile males are competitive with non-irradiated sperm in fertilizing eggs. In species where female receptivity is normally terminated after the first mating, again it is important that sterile males induce this behaviour. In species where it is predominantly sperm from the last mating that fertilize egg batches, it is important that sterile males are equally capable of maintaining this outcome.

The above considerations have become important since recent advances in biotechnology and molecular biology have suggested alternative means of sterilizing males (Häcker et al., this volume). For example, the use of gene-silencing techniques (Nowak 2003) to “switch off” a gene essential for sperm development could well induce true sterility. However, unless the male accessory gland product that “switches off” female receptivity is transferred during mating, these techniques would only serve to create a situation where the released males had little or no impact on the target population (Hendrichs and Robinson, this volume).

By way of contrast, Gould and Schliekelman (2004) suggested a range of novel molecular approaches to sterility that cause lethality in the progeny of released males. Such approaches are unlikely to encounter problems in generating the envisaged impacts. However, as stressed by Gould and Schliekelman, it is important that molecular biologists remain in dialogue with field entomologists so that practical outcomes are optimized. These authors noted that closer collaboration existed during the early period of SIT and autocidal programmes than often exists today between laboratory-based researchers and field ecologists, especially with the latter now an “endangered species” in many countries. Burt (2003) discussed some recent advances in molecular biology, with far-reaching and possibly profound implications for genetic engineering or suppression of natural populations. These revolutionary ideas address the potential of removing the need to mass-rear or irradiate insects before releasing engineered individuals into target populations. On the other hand, such self-sustaining approaches have the disadvantage that they aim at leaving an irretrievable “ecological footprint”, require regulatory approvals, and often face public opposition to the release of transgenic insects (Häcker et al., this volume). Furthermore, unlike radiation, which is a random physical process, molecular approaches include the likelihood of resistance development (Hendrichs and Robinson, this volume).

2.3. Is It Essential That Females Mate Only Once?

Conceptually and operationally, it is simpler if females of the target species mate only once. Initially, E. F. Knipling thought that monogamy was desirable, but later realized that it was not of central importance (Knipling 1955, 1979; Klassen and Vreysen, this volume; Lance and McInnis, this volume). Actually, monogamy can be a significant constraint where migration introduces inseminated females from outside the sterile-male-release area (Barclay, this volume).

In species where females are monogamous, it is essential that sterilized males evoke the same response as normal males during mating to terminate further receptivity by the inseminated female. The competitiveness of the released male is then measured by the difference between the two ratios — sterilized males to normal males versus field females that have been inseminated by the two classes of males.

Multiple matings complicate the situation, but do not disqualify a pest from being a candidate for the SIT. In the latter case, the issue centres around sperm viability and competitiveness in fertilizing eggs, and the competitiveness of sterile males for second or subsequent matings. However, for tsetse flies *Glossina* spp. (Curtis 1968), females mated first to an irradiated male, and then to a non-irradiated male, were less than 50% fertile, just as the reverse order of mating produced greater than 50% fertility. Curtis also addressed another special problem with a viviparous female containing a mix of dominant lethal and normal sperm — an embryonic death might affect the time of the next ovulation. It turned out that this is only a minor problem, and, in the event of an early embryonic death emptying the uterus, the time before the next ovulation is advanced only from the normal 9 to 7 days.

2.4. *Should Released Insects Be Fully Sterile?*

There is little doubt that released females should be fully sterile — not so much for ecological or operational reasons, but for good public relations and to avoid potential litigation or compensation claims. Fortunately, for the majority of species of Diptera against which the SIT is deployed, females require a lower dose than males for complete sterilization, although for a few groups of insects this is not true (Bakri et al. 2005). However, where suppression and not eradication is the objective, males need not be as sterile, especially if the higher dose required for complete sterility significantly reduces competitiveness (Toledo et al 2004; Bakri et al., this volume; Lance and McInnis, this volume; Marec et al., this volume; Robinson, this volume). The objective of the SIT, like any genetic control stratagem, is to impart a genetic load to the target population. If that can be imparted more efficiently through the release of fewer but more competitive males, that are not fully sterile, then that must be the favoured strategy.

2.5. *Does SIT Application Require Isolated Populations or an Area-Wide Approach?*

The SIT, and genetic control methods (as well as pheromone-based mating disruption), are generally sensitive to the effects of immigration, particularly the incursion of females already mated to wild-type males, e.g. studies on compound chromosome strains of *Drosophila* sp. (McKenzie 1976, 1977). In this situation, monogamy can be disadvantageous since an immigrant inseminated female, immune to the abundance of sterile males, can produce fertile offspring (Barclay, this volume). Apparently, the immigration of inseminated females was the cause of only limited success in a large-scale trial on *Culex quinquefasciatus* Say (then known as *C. fatigans* Wiedemann) conducted by the WHO/ICMR in villages in India during the 1970s (Curtis 1976). Immigration was also a negative factor during trials against *Anopheles albimanus* Wiedemann in El Salvador. In one trial an isolated population was eliminated (Lofgren et al. 1974), but in a larger trial immigration reduced the efficacy (Dame et al. 1981), and suppression was achieved only after increasing the release rate of sterile males (Benedict and Robinson 2003).

The negative impact of immigration on the efficacy of the SIT can be countered by applying the technique on an area-wide basis (Hendrichs et al. 2007; Klassen and Vreysen, this volume). For a newly established pest population, such as a recent introduction of an exotic pest, the target area is much less extensive than for an endemic and widespread pest. However, the releases need to extend beyond the target area, taking into account known distribution, habitat suitability, and the pest's dispersal capacity (Barclay et al. 2011).

There would be very few situations where it would be appropriate for a single beneficiary, e.g. owner of a single orchard or farm, to use the SIT independently (Klassen and Vreysen, this volume). Area-wide approaches require organization, coordination, and importantly, financial backing. To provide those resources, the imposition of a levy on stakeholders/producers may be considered (Dyck, Reyes Flores et al., this volume). However, in many situations, some individuals would prefer not to contribute to area-wide control, either because of a perceived loss of independence or a preference for alternative measures (Krafsur 1998). Often the actual or potential beneficiaries of the SIT are farmers, a group that traditionally is independent-minded; and it is inevitable that some would robustly resist making mandatory payments.

It is self-evident that populations of organisms on “islands”, either physical (surrounded by water or mountains) or ecological (a patchy distribution of suitable habitat), are isolated to varying degrees from gene flow (Krafsur and Ouma, this volume). The “island” concept might include urban mosquito populations (where the target species is absent in the surrounding countryside) as a form of ecological island population; their suppression or eradication would benefit many people (Curtis 1976). Such situations present attractive targets. Isolation ensures that the method is at its most economical. However, while long-distance dispersal of the target pest is a disadvantage in any programme releasing sterile insects, imposing an area-wide approach and “barrier zones” can, in suppression programmes, accommodate certain levels of immigration (Hendrichs, Vreysen et al., this volume). If barrier zones are “reasonable”, and the costs and benefits remain favourable, physical barriers to gene flow have not proved to be absolutely necessary.

In terms of an area-wide approach to release strategies and impact, an interesting contrast can be made between biological control and the SIT (Hendrichs, Enkerlin et al., this volume). Box 3 illustrates the enormous regenerative powers of some insect species when colonizing a vacant niche.

2.6. Is Eradication the Only Objective When Using the SIT?

The term “eradication” may be interpreted in a variety of ways. For example, for the World Health Organization, it necessitates the removal of every last individual of a species on the earth (Heymann 2006). Range-wide species extinctions are a natural, indeed inevitable, consequence of the evolutionary process (Wilson 1992). Mankind has been responsible for many accidental, but few deliberate, “eradications”.

On the other hand, eradication at the population level, such as presented by Newsom (1978), is commonly used in plant protection:

Eradication is the destruction of every individual of a species from an area surrounded by naturally occurring or man-made barriers sufficiently effective to prevent reinvasion of the area except through the intervention of man.

Newsom (1978) argued (with some cause given the containment mode of the programme at the Mexico-USA border at the time) that eradication of the New World screwworm *Cochliomyia hominivorax* (Coquerel) in the USA using the SIT had been an “abysmal failure”. However, there should be little argument now, using Newsom’s own definition, that populations of the New World screwworm have indeed been eradicated, not only from the USA, but also from Mexico, and all of Central America (Hendrichs, Enkerlin et al., this volume; Hendrichs, Vreysen et al., this volume; Vargas-Terán et al., this volume).

Box 3. Comparison between the SIT and Classical Biological Control for Area-Wide Control of a Pest

Both pest management tactics require an area-wide impact to be practical, but operationally, the procedures to achieve this outcome can be quite different. For example, in August 1996 the South African tephritid bitou bush seed fly *Mesoclanis polana* (Munro) was released at two sites, some 300 km apart, along the eastern seaboard of Australia to control seed production by the invasive weed, bitou bush *Chrysanthemoides monilifera rotundata* (L.) (Edwards et al. 1999, 2009). In total, 124 adults of mixed sexes were liberated (67 at one release site, 57 at another). By October 1998, the species had occupied virtually the entire range of bitou bush, a distance of over 1200 km (Edwards et al. 1999), establishing vast populations in the process. Thus, within 2 years, these two miniscule founding populations displayed exceptional rates of dispersal, located and colonized scattered and quite isolated pockets of bitou bush, and in the process traversed vast stretches, even cities like Brisbane, that contain no host plants. In May 2004, a survey of six sites, along 700 km of the New South Wales coastline, revealed that 98% of all flowerheads were attacked by *M. polana*, with a mean of 12 eggs laid in each (P. B. Edwards, personal communication). It would be a sobering thought to contemplate the effort and efficacy of rearing and releasing sufficient sterile males of *M. polana* along the eastern coastline of Australia to reverse the phenomenal outcome achieved by the bitou bush seed fly following its release. Yet, we have no reason to doubt a similar or even greater dispersal and reproductive capacity of an invading pestiferous tephritid such as the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) which, unlike the bitou bush seed fly, is polyphagous with an enormous host range. One is a beneficial insect, the other a pest, but only because of the economic status bestowed by their hosts.

Where repeated immigration of fertile females occurs, either natural or human-made, eradication may need to be followed by preventive releases in areas of high risk of pest incursions (Hendrichs, Vreysen et al., this volume). The recurrent invasions of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) into California represent such a situation (Krafsur 1998). The preventive release for 25 years of sterile flies over the Los Angeles basin, where most incursions occur, has avoided the establishment of the Mediterranean fruit fly in the face of repeated human-assisted incursions (Dowell et al. 2000). Although Carey et al. (2017) claim that there are established Mediterranean fruit fly populations at “undetectable levels” in California, the validity of the concept that populations with a high reproductive rate can remain undetectable for years under favourable host and climatic conditions has not been accepted by trading partners, and has been challenged by McInnis et al. (2017) and Shelly et al. (2017). Thus, in such situations, the SIT is an effective preventive, rather than an eradication, tool to maintain the pest free status (Dowell et al. 2000; Hendrichs, Enkerlin et al., this volume).

A final example of accommodating the objectives of an AW-IPM programme integrating the SIT, by recognizing immigration, is the pink bollworm *Pectinophora gossypiella* (Saunders). The cotton-growing areas of the San Joaquin Valley, California, were protected for decades from infestation by the pink bollworm through the implementation of an AW-IPM programme in which the SIT was a key component in containing the pest. The SIT also played a key role in the subsequent eradication of the pink bollworm from the USA and northern Mexico (in combination with growing transgenic cotton and the use of pheromones for mating disruption) (Staten and Walters 2021).

The eradication of an established population of a pest species is a challenging objective. Even deciding whether or not to attempt eradication is not a simple matter. Myers et al. (2002) stated that:

... evaluation of the ecological and economic costs and benefits of removing an exotic species is difficult, and often the benefits are exaggerated and the costs are understated.

Nevertheless, there is no doubt that, in the case of incipient outbreaks of invading non-native pests, eradication is the most cost-effective alternative when compared with allowing the permanent establishment of a new pest that will have to be suppressed continuously. Furthermore, in view of its inverse density-dependence, the SIT has been shown to be particularly suited to eliminate invasive pest populations in an environment-friendly way (Hendrichs, Enkerlin et al., this volume).

While the SIT does become more effective as the target population dwindles and the ratio of sterile to fertile males increases, this positive attribute of the SIT should not condemn it to be exclusively an eradication option. Krafus (1998) noted:

... because SIT can lead to eradication, anything less may come to be judged a failure.

In this sense, the necessity of using the SIT only for eradication is clearly a misconception.

Frequently, other strategic options, such as containment, prevention and suppression, rather than eradication, are the objective of applying the SIT (Hendrichs, Vreysen et al., this volume). The objective of suppression, instead of eradication, is often necessitated by the undesirability of establishing quarantines, the lack of isolation resulting in unacceptable levels of immigration, as well as other factors. In this common situation, the integration of the SIT into AW-IPM programmes, such as those for several moths and fruit flies, demonstrates that the SIT can be an important component of such suppression programmes (Hendrichs, Vreysen et al., this volume).

2.7. Is the SIT a Stand-Alone Technology or Part of an Area-Wide IPM Strategy?

The SIT is not a stand-alone technology, and thus it has to be integrated in various degrees with other control tactics (Simmons et al., this volume; Mangan and Bouyer, this volume). Even in the North American New World screwworm regional eradication programme, there has been some integration with other suppression measures, such as dressing infested wounds with larvicides, mobilizing ranchers to report cases of infestation, as well as cultural and quarantine activities (Klassen et al., this volume; Vargas-Terán et al., this volume). In contrast, all the various fruit fly

programmes that release sterile flies range from area-wide suppression to eradication; the SIT for fruit flies is integrated with baits, lures, and cultural practices (Enkerlin, this volume; Klassen et al., this volume; Mangan and Bouyer, this volume).

One impressive example of integrating the SIT into AW-IPM, where the goal is sustained suppression, is the Okanagan-Kootenay Sterile Insect Release (OKSIR) Program (codling moth *Cydia pomonella* (L.)) in British Columbia, Canada; it uses a “knowledge-based” approach (Simmons et al., this volume). This programme requires the cooperation of commercial fruit growers and property owners. The programme is funded through local taxation; it obtains 60% of its funding from property owners in the community and 40% from commercial growers (OKSIR 2018; Seymour 2018; Nelson et al. 2021). At various times the OKSIR has applied the following tactics (*Bt* sprays were deemed to be ineffective):

- Various tree-husbandry practices and field hygiene
- Legal authority to enter orchards and residential properties to inspect for infestation and issue control orders for fruit stripping and tree removal
- Initial chemical sprays to suppress a high pest population
- Initial sex pheromone mating disruption in some orchards
- Sex pheromone traps used for monitoring (about one trap per hectare)
- Twice-weekly sterile moth releases
- End-of-season banding of host trees (to trap mature larvae) in some orchards; later the strips are removed and destroyed).

Although eradication was the initial objective, no quarantines were implemented, and thus this is no longer deemed practical as a short-term solution. Instead, a sustainable programme has evolved, which has successfully implemented the revised objective to:

. . . substantially reduce the amount of toxic pesticides currently used to control [suppress] codling moth, and that means a more competitive fruit industry and healthier local environment for everyone.

From 1991 to 2016 there was an estimated 96% sustainable reduction in insecticides used against the codling moth in the target areas (Nelson et al. 2021). Two important take-home messages emerge from the Canadian codling moth OKSIR Program: informed stakeholders are not hampered by misconceptions, and constraints are viewed as challenges to be met and overcome.

2.8. *Could Eradication Have Deleterious/Unanticipated Consequences?*

Eradication of a pest population, through whatever means, could conceivably have unexpected consequences. If the species is exotic to the area, and the incursion is small, eliminating the invasive population will re-establish the original situation. However, at the other end of the scale, eradication of a widespread indigenous species, such as a tsetse or screwworm species, may lead to undesirable impacts that need to be considered (Nagel and Peveling, this volume). Myers et al. (2000) provided examples of “secondary” consequences of eradication, following the eradication of exotics from islands, such as the removal of vertebrates, rats, and rabbits. These authors point out that reversing the changes to native communities following the eradication of exotics

is not a trivial undertaking, and requires a sophisticated ecological understanding. In general, however, the negative externalities of the SIT are less than those of most alternative pest suppression tactics, especially pesticides (Nagel and Peveling, this volume).

3. SOME CONSTRAINTS ON THE SIT

3.1. Changing Contextual Framework for the SIT

In spite of the successes of significant AW-IPM programmes integrating the SIT against various moth and fruit fly species (Simmons et al., this volume; Enkerlin, this volume), the successful eradication of the New World screwworm in North and Central America (Vargas-Terán et al., this volume) remains a primary model, in terms of its size, economic importance and durability, for most SIT endeavours. Nevertheless, several changed economic and social circumstances, especially over the past 40 years, suggest that even this highly successful programme would encounter difficulties if it were launched today. Changing social, economic, and political circumstances have probably reduced the feasibility of implementing similar-sized programmes elsewhere in the world. In recent times, perhaps of greater relevance as successful SIT models, are the bi-national USA-Mexico pink bollworm programme, and the on-going Mediterranean fruit fly AW-IPM programmes in Latin America.

The successful North American screwworm programme has been characterized as having a pragmatic and opportunistic “can do” approach. For example, it adapted a “mothballed” hangar at a well-sited but unused air force base in southern Texas. This facility did not demand the construction and safety standards currently required of a similar facility. Today, in most countries, occupational health and safety issues, and general worker conditions, are more stringent, and remuneration is more substantial, than in the 1960s. Public liability, insurance premiums, and tendencies to litigate have increased enormously in the past 40 years. Such factors mean that the initial outlay costs for constructing and operating a mass-rearing facility are now much higher. Nevertheless, a facility to rear the New World screwworm has been built in Panama, and several fruit fly rearing facilities are being constructed.

The decline in primary-producer contribution to the gross domestic product (GDP) of many developed nations (now often less than 3%, according to the World Bank) has reduced the political influence of farmers (Europe, Japan, and the USA remain exceptions to this trend). This decline, together with a greater emphasis on the “user-pays principle”, aggravates the situation. In cases where pest eradication is the principal objective, reinvasions due to the increased global movement of people, livestock and materials, and threats of bio-terrorism, all serve to reduce the prospects of a sound economic return on the not-insignificant initial outlay. Also, as mentioned earlier, large up-front costs, and the need for stringent quarantine measures that can interfere with trade and the movement of goods, may be serious disincentives to invest in the SIT for eradication of large, established populations. However, this is not the case for the application of the SIT to eliminate outbreaks of invasive pests (Kean et al. 2018; Hendrichs, Enkerlin et al., this volume).

A general decline in financial support for relevant research and development (R and D), compared with that available to the US screwworm programme during the 1960s and earlier (Krafsur 1998), linked to some of the factors listed above, will often mean that less is known about future target populations.

The construction of multi-purpose mass-rearing facilities could lessen the impact of some of the above negativities, and provide significant economies (Fisher 2002). However, in turn, such centralized facilities create new problems, such as increased complexity in management and greater technical challenges relating to the competitiveness of released males. The logistics of material supplies for mass-rearing, and transport of sterile insects to release sites, are also likely to represent greater challenges. Certainly many of the above considerations would impact on risk-adverse decision-makers in Australia, New Zealand and Canada, and probably the European Union, regarding the wisdom of conducting area-wide eradication programmes based on the SIT (Vargas-Terán et al., this volume).

Realistically, if an area-wide campaign were to cover transboundary populations in diverse countries in a region like South-East Asia or Africa, the political, logistical, and ecological challenges would be significant. Such considerations have meant that, in Australia (for area-wide eradication of an existing pest such as the Australian sheep blow fly *Lucilia cuprina* (Wiedemann), or pre-emptive construction of a mass-rearing capacity to cope with an intrusion of the Old World screwworm *Chrysomya bezziana* (Villeneuve) (Vargas-Terán et al., this volume)), the SIT is effectively not on the agenda, in spite of policies to the contrary. Nevertheless, the SIT continues to be used as a rational approach to suppress several fruit fly related problems in Australia and elsewhere (Fisher 1996; Meats et al. 2003; SITplus Partnership 2018).

Compared with most other pest management tactics, the SIT is uniquely affected by another constraint — limited independent and robust experimental field data to evaluate the short- and long-term impact of released sterile insects on population dynamics. Information is often inadequate on key issues such as competitiveness, dispersal rates, and density dependence (Itô et al., this volume); however, data obtained on the Mediterranean fruit fly in Guatemala provide insight into pest population suppression and competitiveness in large-scale field programmes (Rendón et al. 2000, 2004). As Krafsur (1998) noted, many experimental SIT trials have striven to isolate and reduce a target population. A combination of suppression measures are often integrated to achieve this outcome (Mangan and Bouyer, this volume; Nagel and Peveling, this volume). Thus, frequently, according to Krafsur (1998):

... the effects of sterile male challenge are confounded by other treatments.

In this sense, AW-IPM programmes that integrate the SIT, even highly successful ones like the New World screwworm programme in North America, are usually not designed to test hypotheses, but to achieve specific operational outcomes. While this strategy is understandable, it has a serious downside — sometimes little is learned from SIT successes (and failures) that could be applied to other pests.

In spite of the limitations imposed by changes in attitude and resources in the world, the SIT flourishes for species for which the technology is well established, such as the New World screwworm, and various moth and fruit fly pests.

Some encouraging new developments include a revival of interest in the application of the SIT for *Aedes* spp. and *Anopheles* spp. mosquitoes (Touré et al. 2004; Bourtzis et al. 2016; Lees et al., this volume), and in addition two species of tsetse, *Glossina austeni* Newstead and *Glossina palpalis gambiensis* Vanderplank, have been added to the list of targets against which the SIT has been successfully applied (Vreysen et al. 2000, 2021). Also significant is the exploration of opportunities for commercially viable sterile insect production facilities (FAO/IAEA 2008) that hopefully will serve as examples and, in time, provide alternatives to government-funded and government-controlled programmes.

3.2. Is the SIT Too Expensive, or Does It Fail the “User-Pays” Principle?

When control options in AW-IPM programmes are being assessed, whether to suppress or eradicate an existing pest population or deal with an incursion, the question of cost is often foremost. The cost of SIT strategies generally will include the following: expense for monitoring and some other form of control to reduce an initial high target population, and cost of purchasing and releasing the sterile insects. In many programmes, the cost of providing and releasing sterile insects comprises a high proportion of the costs. However, model inputs show that other costs may outweigh the cost of sterile insects (Mumford, this volume). For example, in the case of an eradication programme, proof of pest free status required by a trade partner may drive up trapping costs significantly.

In cases where a reliable and economic supply of sterile insects does not exist, the “deal breaker” need not be just the total cost of the sterile insects, but the substantial upfront investment needed to construct and equip a new production facility. The start-up time for establishing a colony and reaching sufficiently high production is also a factor. However, the risk can be somewhat spread at each step in the SIT-development pathway by collecting evidence to assess the merits of further investment so that it becomes an incremental process: if progress is not promising, withdrawal is possible along the way (FAO/IAEA 2008). For example, at first, small pilot projects are carried out to assess the feasibility of the approach and to validate the technology. Moreover, when planning a mass-rearing facility, this can follow a modular design as described by Tween (1987), where construction of new rearing modules around a central core only proceeds if the demand for sterile flies gradually expands.

Increasingly, the SIT has been used in suppression or seasonal control programmes in a manner similar to pesticides, e.g. codling moth management in Canada, Mediterranean fruit fly in Croatia or Israel, false codling moth *Thaumatotibia leucotreta* (Meyrick) in South Africa, and onion maggot *Delia antiqua* (Meigen) in The Netherlands. The onion maggot control programme is the only example of an ongoing long-term (over 30 years) suppression programme where growers pay a private company to monitor as well as produce and apply the sterile insects. This programme faced the challenge of those who would turn to the SIT only when other options had failed, and therefore the population of the pest was too high to achieve good results using the SIT (Loosjes 2000). Also, due to rotation of crops and some “free-riders”, there is no coordination among growers or area-wide approach, and thus no accumulated benefit to the users of the SIT, only a season's benefit. Furthermore,

early support from the Dutch government, in recognition of the enterprise as an environmental business, was terminated due to a change in policy. The loss of this funding eliminated any recognition of public benefits from the reduced use of pesticides, and also caused some users to wonder if the pull-out of the government reflected on the overall product or concept. In spite of these setbacks, the private supply of sterile onion maggots has been maintained, the surface treated has gradually increased to an aggregate area of ca. 10 000 hectares (40% of the onion production), and the programme continues to be successful (Everaarts 2016).

Several large-scale eradication programmes have been cost-effective. Without doubt, successful programmes such as the North and Central American screwworm programmes have proved to be enormous economic successes (Vargas-Terán et al., this volume). The same applies to the Mediterranean fruit fly containment programme that, for 40 years, has maintained Belize, Mexico, USA and ca. half of Guatemala free of this pest, with annual USD multi-thousand-million [multi-billion] benefits to the respective horticultural industries (Enkerlin et al. 2017). These successes have served to ensure a serious evaluation of other potential programmes. However, the problem of cost is more complex than just raising the substantial resources to construct and operate a mass-rearing facility, and conduct the release and monitoring activities. The risk of an eradication venture failing, with no return on investment, can daunt all but the hardest of optimists. However, a suppression strategy can represent a viable fall-back position, as shown by the Canadian codling moth programme, and some other moth and fruit fly programmes.

One must keep in mind, in any case, that since the SIT does not entail any intellectual property rights (IPR) at this stage, there is little incentive for private enterprise to participate, other than as a “hired hand”. Profits must come from the sale of services and sterile flies, as there is little scope for sale of assets of such a company compared with other types of businesses (Barnes 2007; FAO/IAEA 2008). However, in the case of long-term suppression, preventive or containment programmes, that continuously require sterile insects, the financial risk to private investors would be lower than in eradication programmes, where the demand terminates as soon as eradication has been achieved (FAO/IAEA 2008; Simmons et al., this volume; Enkerlin, this volume; Hendrichs, Vreysen et al., this volume).

It can be concluded, in terms of cost-effectiveness, that area-wide application of the SIT is not too expensive when all benefits are quantified, and beneficiaries better understand the technology and participate in the programme (Kruger 2021). In an increasingly “user-pays world”, it is equally important to convince those who will capture the benefits to contribute resources in proportion to their benefits. Nevertheless, the most vexatious financial issue is ensuring that all those who capture the benefits pay equitably (Mankad et al. 2021). In suppression programmes, the beneficiaries often contribute to programme costs, e.g. the codling moth OKSIR Program in Canada, where growers and property owners cover all of them (Nelson et al. 2021; Simmons et al., this volume), or the Mediterranean fruit fly programmes in Latin America and South Africa where they pay part of them (Dyck, Reyes Flores et al., this volume; Enkerlin, this volume).

The actual public benefits have usually not been well-measured to date, with some exceptions such as the evaluation in Madeira of indirect impacts on reduction of pesticide use, preservation of cultural heritage, and support of tourism (IAEA 2005).

Unintentional subsidies by government for the production of sterile insects used in third-party programmes will certainly discourage private investment in the sterile insect production sector (Bassi et al. 2007; FAO/IAEA 2008). This could lead to further use of government funds for the SIT, even in those cases where stakeholders are willing to pay their fair share of programme costs.

Much more problematic is the task of identifying the appropriate financial resources, and securing the necessary budget, for programmes that have wider benefits or where the beneficiaries could not afford the cost. For eradication programmes, often the only realistic source is probably the public purse — governments in developed countries, and support from international aid agencies in less-developed countries (Dyck, Reyes Flores et al., this volume). Even when the identity of beneficiaries is clear, if the benefits are not sufficiently appreciated, users are unlikely to pay. For example, in Australia, various attempts to develop a genetic control programme for the Australian sheep blow fly (Foster et al. 1993; Krafur 1998; Klassen and Vreysen, this volume), either on the mainland or the island of Tasmania, were abandoned, either because the cost was deemed to be too high (Waterhouse 1962), or because it was difficult to obtain the necessary financial backing (King et al. 1992).

In conclusion, AW-IPM programmes that release sterile insects are often susceptible to the “user-pays principle”, but many cases fall outside this approach. It will be just as important to establish the “public good” in privately funded programmes, and obtain partial support for that benefit in the future, as in the past it has been to identify and engage private beneficiaries in government-led programmes.

3.3. Adverse Population, Ecological, and Behavioural Parameters

The suppression effects of flooding a natural insect population with sterile males depend on a suite of factors. Difficulty in adequately satisfying some of these could amount to a serious constraint in successfully applying the SIT to a particular pest. However, articulating such issues can sometimes transform a constraint into a challenge, and ultimately into an opportunity. Constraints and complementary opportunities can include:

- Large size of the natural target population versus methods of suppressing numbers before releases by other means (e.g. pesticides, mating disruption, sanitation and other cultural interventions), or simply exploiting seasonal fluctuations (Mangan and Bouyer, this volume)
- Migration from non-target populations versus choice of target area to maximize effective immigration barriers (Itô et al., this volume; Hendrichs, Vreysen et al., this volume)
- Low competitiveness of released insects (due to initial laboratory colonization, artificial diets, radiation and shipment damage, artificial colony management conditions over many generations, especially for adults and mature larval stages which may normally enjoy solitary conditions in the field) versus emphasis on quality control (and more natural colony holding, diet and rearing conditions), strain selection or regular injection of new genetic field material into mass-reared colonies, improving sterile male performance, and using probiotics and symbionts (Liedo et al. 2007; Pereira et al. 2013; Sánchez-Rosario et al. 2017; Augustinos et

al., this volume; Bakri et al., this volume; Lance and McInnis, this volume; Parker, Mamai et al., this volume; Parker, Vreysen et al., this volume)

- Adverse impact of released females (sting damage from some fruit flies or biting behaviour of blood-feeding pests, or animal or plant disease-transmitting vectors) (Lees et al., this volume; Nagel and Peveling, this volume) versus genetic means of removing females, preferably early in the life cycle (Franz et al., this volume)
- Frequency-dependent factors affecting competitiveness (i.e. ratio of released to field males) versus release ratios that minimize this effect (Vreysen, this volume)
- Increased ability of field females to discriminate against released males versus exploration of colony management and mass-rearing conditions that mitigate this selection (Miyatake 1996, 1998), and regular strain replacement to minimize risk of discrimination (Hoffmann and Ross 2018; Lance and McInnis, this volume).

It is one thing to identify constraints and the complementary opportunities, but to turn these to our advantage requires long-term research. As noted by Krafsur (1998) and Gould and Schliekelman (2004), conditions for the necessary underpinning strategic research, both in terms of resources, expertise, and collaboration, were more ideal during the 1960s and 1970s. Resources and creative ideas are abundant in molecular genetics (Burt 2003; Häcker et al., this volume), but unless these are linked to field-oriented research in ecology and behaviour, the advantages are unlikely to be captured (Gould and Schliekelman 2004; Itô et al., this volume).

3.4. *Mating Barriers — Serious Constraint on Programmes that Release Sterile Insects?*

For the SIT to work, sterile males must be competitive with the field males of the target population(s) of a pest in seeking mates. If we are dealing with a group of distinct species, or even subspecies with limited interbreeding, it is clear that each taxon will have to be tackled separately for progress to be made. This is especially true if the species in the complex are ecologically equivalent, and where a neighbouring taxon can be expected to occupy the vacated niche (Box 2). If the pestiferous species, perhaps vectoring the same disease, is already coexisting, then there is little to be gained by targeting one taxon with the SIT. In such cases, the specificity of the SIT could be a disadvantage.

The above constraint applies equally to cryptic species, where the situation could be more insidious if the mating barriers are undetected because the relevant biological knowledge is simply unavailable. Even supposedly well-known entities such as major malaria vectors, e.g. *Anopheles gambiae* s.l. Giles (White 1974), were found to harbour morphologically indistinguishable, but genetically distinct, species with important consequences for insecticidal suppression programmes (Paterson 1963). Conversely, raising taxa that are not genetically isolated to species status could unnecessarily discourage SIT practitioners (Hendrichs et al. 2015). To avoid both types of problem, it would be prudent to conduct the definitive test — determine if sterile males compete effectively with field males in the target populations (Parker, Vreysen et al., this volume). In his hybridization experiments, Vanderplank (1947) confirmed that this was the case in his pioneering work on autocidal control of tsetse

(Klassen et al., this volume). Below several situations are described where this critical behavioural test was conducted, demonstrating that the SIT should, and did, work.

Based on morphological, cytological, and allozyme differences, Richardson et al. (1982) postulated that the New World screwworm in Mexico and the USA consisted of a number of sympatric, and generally non-interbreeding, populations. The existence of these “gamodemes” was hotly debated (LaChance et al. 1982), and the subsequent eradication of the pest from these regions argues strongly against the Richardson scenario. The question has been rendered irrelevant, now that all screwworm populations north of the Panama-Colombian border have been eliminated (Vargas-Terán et al., this volume). However, what is relevant is that the Richardson analysis could have been used to stop the successful expansion of the screwworm programme, and thereby denying farmers in North and Central America the enormous economic benefits that the SIT actually provided.

Equally important has been the direct-mating test in northern Africa, following the introduction of the New World screwworm into Libya in the late 1980s). Taylor et al. (1991) examined the “reproductive compatibility” of Libyan flies and the mass-reared strain. They also examined genetic variability (chromosome morphology, homolog pairing and m-DNA restriction-site analyses) of populations from Libya, the mass-reared strain, and extant Central American, Mexican, and Caribbean populations. Their analyses indicated that mating barriers should not prevent the eradication of the Libyan populations using “Mexican” sterile flies. Indeed, the successful programme proved to be one of the landmark achievements of the SIT (FAO 1992; Lindquist et al. 1992; Krafur and Lindquist 1996).

A second example of research being conducted to ensure better mating and genetic compatibility (Feldmann and Ready 2014; Parker, Vreysen et al., this volume), and thus success of the SIT, is provided by the Old World screwworm. Given that the species is found over a large geographical range, possible incursions of this fly might be refractory to the SIT when using a colony established from a distant population. In response, samples of screwworms from southern Africa, the Middle East, and South-East Asia were subjected to various analyses — allozyme (Strong and Mahon 1991), cytological (Bedo et al. 1994), cuticular hydrocarbons (Brown et al. 1998), and laboratory hybridization tests (Mahon 2002a; J. P. Spradbery, unpublished data). No indication of discontinuities, that might indicate the presence of sibling species, was found. Subsequently, analyses of mitochondrial DNA (Hall et al. 2001) resulted in a similar conclusion. However, with the increased resolution of the technology employed, these authors detected the existence of two mitochondrial “races”, one in sub-Saharan Africa and the other extending from the Persian Gulf to South-East Asia (Feldmann and Ready 2014). Thus, if the SIT were to be implemented in Australia, it would be prudent to establish a colony from either the introduced flies or the source population.

The absence of mating barriers could reasonably be assumed where the evidence suggests recent movements of an insect species around the globe, including the Australian sheep blow fly, Mediterranean fruit fly (Cayol 2000), the oriental fruit fly *Bactrocera dorsalis* (Hendel) (Hendrichs et al. 2015), and the codling moth (Taret et al. 2010).

3.5. *Evolution of Resistance to the SIT?*

Insects have shown a remarkable propensity to evolve resistance to chemical challenges used by man in efforts to suppress them. Some species, such as the house fly *Musca domestica* L., certain mosquitoes and whiteflies, are recidivists in that they have evolved resistance to a wide range of insecticides. With this background, it is not surprising that the question is sometimes asked, “Can insects evolve resistance to the SIT?”

Certainly, a species could “escape” if it was able to adopt asexuality. Perhaps only those species that had a pre-existing mix of sexual and asexual modes of reproduction could respond rapidly enough to make use of this mechanism. A sexual species would more likely be driven to extinction before the drastic genetic changes necessary for this process could occur.

A possible caveat to the belief, that an asexual response from an SIT-targeted population represents only a minor threat, is if the cytoplasmic symbiont *Wolbachia* sp. is already present in the species, and plays a role in the determination of sex and the sex ratio. *Wolbachia* is a rickettsia-like bacterium that is found in up to 76% of arthropod species (O'Neill et al. 1997). The presence of these organisms produces a wide range of effects, including conversion of genetic males into functional females, male-killing, cytoplasmic incompatibility, thelytoky, and also may have effects on viability (Bourtzis 2008). Since the effects of an infection with these cytoplasmically-inherited organisms can be so comprehensive, e.g. thelytoky in hymenopteran species (parthenogenesis where the population consists only of females), the implementation of a programme releasing sterile insects could cause the conversion of an apparently sexual species into an asexual one through the elimination of the uninfected, i.e. the sexual, portion of the population.

The dramatic effects of *Wolbachia* vary between groups of species, with perhaps conversion to thelytoky being an extreme effect. Thus, while consideration should be given to the possibility of a programme being thwarted by the effects of *Wolbachia* or similar symbionts, existing programmes have not encountered such problems. More often, *Wolbachia*-induced cytoplasmic incompatibility is being applied as a tool for vector population suppression in a self-limiting way, analogous to the SIT (known as the incompatible insect technique (IIT)) (Lees et al. 2015). However, female removal is critical for such *Wolbachia*-based IIT strategies to be sustainable, but existing mechanical separation is labour-intensive and does not result in the required complete elimination of females, and is therefore not practical for application on a large scale. On the other hand, combining the SIT and the IIT against vectors such as mosquitoes, where male-only releases are an absolute prerequisite, assures that any accidentally released females are sterile, while simultaneously benefitting from the pathogen interference properties of *Wolbachia*, thus avoiding any possibilities of disease transmission by such females (Bourtzis et al. 2016). Alternatively, *Wolbachia* can be used in a self-sustaining way as a means of “driving” desirable genotypes into populations, although such a population replacement is irreversible (Turelli and Hoffman 1999; Bourtzis et al. 2016; Robinson, this volume).

While an asexual response is considered unlikely, and there are certainly no examples of it, the form of resistance to the SIT more commonly considered (at least to be a possibility) is that females of the target population could evolve behavioural

mechanisms to avoid mating with mass-reared sterile males. The argument for such a possibility has been put forward most strongly by Boesiger (1972), who considered it almost inevitable that, while early releases of sterile males might be highly efficacious, the survivors would be enriched for genotypes capable of avoiding sterile males, and thus selection for this ability (McInnis et al. 1996).

Through genetic divergence, or physiological changes associated with mass-rearing, there should be ample “markers” for field insects to discriminate against mass-reared insects, but the question remains, “Is it likely?” The likely outcome is that in eradication programmes the population will become extinct before resistance has evolved. On the other hand, in suppression or containment programmes, such selection is usually countered by certain levels of immigration of already mated females. Indeed, AW-IPM programmes integrating the SIT have been active for decades against both the Mediterranean fruit fly and the New World screwworm. To date there is no evidence that resistance has developed, and the SIT remains effective for both species (Krafsur 1998). Similarly, the SIT has been deployed against other species as well, and again there is no evidence to suggest the evolution of resistance to the SIT (but note comments by Hendrichs and Robinson, this volume; Lance and McInnis, this volume).

A possible exception is a study on the melon fly *Zeugodacus (Bactrocera) cucurbitae* (Coquillett). Hibino and Iwahashi (1991) examined the mating behaviour of the melon fly using males from a long-term colony, and females from two islands in the Ryukyu Archipelago of Japan. Females from Okinawa Island (where SIT releases had been ongoing for some time) discriminated against mass-reared males, whereas females from Ishigaki Island, not yet exposed to SIT releases, did not. This finding was contrary to an earlier study performed before implementing the SIT, wherein Koyama et al. (1986) found that the mass-reared strain and those from Okinawa mated at random. Hibino and Iwahashi (1991) interpreted this as evidence that Okinawa females had “evolved sexual isolating barriers” to the mass-reared males (note comments by Itô et al., this volume).

Clearly, care should be taken to document any changes in behaviour and mating compatibility during the course of a programme releasing sterile insects. However, perhaps it is more appropriate simply to avoid the problem by maintaining the genotypic variation within the mass-reared colony as similar as possible to that of the target population (Hoffmann and Ross 2018). This can be achieved by “refreshing” the genetic variability within the mass-reared strain, such as the regular replacement of the mass-reared New World screwworm strain with field-derived colonies (Mangan 1992), or the regular infusion of genetic material from the target population into the culture (Parker, Mamai et al., this volume).

Recent advances in our ability to “cryopreserve” the embryos of recently colonized strains of species of economic importance where the SIT is either ongoing or could potentially be employed (Leopold et al. 2001), should facilitate this process. Mahon and Leopold (2002) reviewed the potential uses of this technique within programmes that integrate the SIT, one of which would be to prevent the “deterioration” of colonies through genetic changes brought about by long-term selection in mass-rearing. The suggested procedure is to cryopreserve batches of embryos as soon as a newly established colony becomes sufficiently laboratory adapted to be suitable for mass-rearing. After some generations, the mass-reared colony could be discarded and a

fresh batch of embryos revived to re-establish the colony (Parker, Mamai et al., this volume).

3.6. Poor Competitiveness of Released Insects Can Be a Major Constraint

In this volume, many chapters address aspects of “competitiveness”: Bakri et al., Barclay, Hendrichs and Robinson, Itô et al., Klassen et al., Lance and McInnis, Lees et al., Marec et al., Parker, Vreysen et al., Pereira et al., Robinson, and Vreysen.

Competitiveness is an important feature of released insects. Poor competitiveness, when it occurs, contributes to an increased cost of the SIT, and cost is perhaps the major constraint to a more general application of the technique. Superficially, many of the costs of any successful AW-IPM programme that releases sterile insects may appear to be fixed, but the size of the required mass-rearing facility, and the costs of the diet and insect release operations, are all dependent on the competitiveness of the sterile males. Reduced competitiveness inflates the cost if, as occurs often, mass-reared and sterilized insects perform poorly in the field in terms of longevity, flight behaviour or ability to compete for mates. Consequently, the programme must commit to produce and release more insects than would be required if released insects were equal to field (wild) insects in their mating propensity and capability.

Lance and McInnis (this volume) suggest that the competitiveness (as defined by Haisch 1970 and Fried 1971) of Mediterranean fruit fly sterile males may in very extreme cases be less than 1%. This implies that more than 100 sterile males are required to equate to the mating behaviour of a single wild (fertile) male. Clearly, a slight improvement in competitiveness would have a dramatic effect on the costs and benefits of the SIT. Progress in developing semiochemical, nutritional, hormonal and other post-factory treatments to improve sterile male performance has been essential in addressing this major constraint (Pereira et al. 2013).

The low tolerance to fruit damaged by Mediterranean fruit flies, and the relatively low cost of insect production for the SIT, provide positive benefit/cost ratios for this species. However, for other species, this may not be the case. For example, Australian authorities are re-evaluating appropriate preparedness strategies to respond to a potential future incursion of the Old World screwworm (Vargas-Terán et al., this volume). In an SIT trial conducted in Malaysia (Mahon 2002b), the competitiveness of mass-reared and irradiated Old World screwworms was approximately 4%. A re-analysis of a similar trial in Papua New Guinea performed by Spradbery et al. (1989) yielded a similar value (R. J. Mahon, unpublished data). If competitiveness is calculated in this way, the merits of SIT integration could be questioned, but much depends on the programme costs and benefits in relation to alternative tactics that can similarly achieve eradication of the invasive population. Further work must be done to improve competitiveness, thereby ensuring that the costs and benefits of the SIT for this species remain positive (Parker, Vreysen et al., this volume). Unfortunately, increasing the number of sterile insects released (and hence the release:wild ratio) may not be the simple remedy for low competitiveness, especially if there is a negative relationship between the ratio of released:wild males and mating success, as suggested in field trials of sterile tsetse *Glossina palpalis gambiensis* (Rogers and Randolph 1985) and translocation-bearing males of the Australian sheep blow fly (Mahon 1996).

4. CONCLUSIONS

The SIT has proved to be a robust and “green and clean” technology, yet the range of species to which it is presently being applied is relatively limited. The outstanding successes of the SIT with the New World screwworm in North and Central America, and in Libya (Vargas-Terán et al., this volume), as well as with the Mediterranean fruit fly and other species of fruit flies and moths in a number of regions of the world (for suppression, eradication, containment, or prevention) (Enkerlin, this volume; Hendrichs, Vreysen et al., this volume), raise questions about why the SIT has fallen short of the high expectations for the technology.

Some misconceptions are partly to blame but, in general, these seem to be more like irritants than real impediments. Two strengths of the SIT are its specificity, and the absence of negative externalities that haunt other pest management tactics such as synthetic pesticides and, to a lesser extent, classical and augmentative biological control. Concern about residual irradiation, or the production of toxic metabolites, is discussed primarily to dismiss this issue as lacking foundation. Other common misconceptions identified include: the need for monogamous females and for released males to be fully sterile; maintaining that eradication is the only possible goal; the SIT is too sophisticated for developing countries; and failure to recognize the SIT as a valuable component of area-wide IPM strategies. In each case, we concede that these warrant analysis, but conclude that each is not an impediment for a successful programme that releases sterile insects.

The identified constraints pose more serious threats to extending the SIT to other insect pests. In particular, we recognize that the SIT and other genetic methods of pest control are knowledge-based technologies. Thus, SIT application is complex and management intensive, requiring dedicated and effective managers to be successful (Vreysen et al. 2007; Dyck, Reyes Flores et al., this volume). Failure of the public to understand the nature of genetic material, and how interventions to disrupt the orderly inheritance or expression of this genetic information can be achieved, can introduce fear of the unknown. Financial considerations rank high on the list of constraints. The need for large upfront expenditure, risk aversion (failure to get any return on a failed eradication campaign), and rigid application of the beneficiary-pays principle in some countries without establishing the “public good” of such programmes, have proved to be serious disincentives for some potential SIT eradication projects that otherwise appeared to be feasible technically.

In the technical arena, the low competitiveness of released males is a serious constraint, especially if not given top priority by managers. Increasingly, detailed quality control manuals are available to assess carefully sterile male behaviour and performance in field cages and the field; also molecular tools and other markers have been developed that allow quantifying sterile and wild sperm presence in females of the target population (Juan-Blasco et al. 2013; FAO/IAEA/USDA 2019; Johnson et al. 2017).

Lack of support for the necessary underpinning strategic research also appears to be an important constraint. Hence, the case for extensive strategic research in ecology, population dynamics, density-dependent regulation, genetics, insect behaviour, and insect nutrition is a compelling one. Raising the competitiveness of released males remains the major research objective for the SIT.

Exciting new developments in molecular biology are being exploited to develop entirely novel genetic tactics, both in support of self-limiting, such as the SIT, as well as self-sustaining approaches that aim at population replacement strategies using gene drives or *Wolbachia* systems (Häcker et al., this volume). Even if the latter do not depend on the release of large numbers of mass-reared and sterilized insects, with all the associated challenges, they have a higher likelihood of resistance development, require regulatory approvals, often face public opposition, and leave an ecological footprint.

5. REFERENCES

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