CHAPTER 3.2.

MASS-REARING FOR THE STERILE INSECT TECHNIQUE

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SUMMARY

Since the sterile insect technique (SIT) relies upon released sterile male insects efficiently competing with wild males to mate with wild females, it follows that mass-rearing of insects is one of the principal steps in the process. Mass-rearing for the SIT presents both problems and opportunities due to the increased scale involved compared with rearing insects for most other purposes. This chapter discusses facility design, environmental concerns, strain management, quality control, automation, diet, sex separation, marking, and storage in relation to rearing for the SIT. The cost of sterile insect production drops rapidly with increasing scale, but the point at which the SIT becomes economic in comparison with other methods will depend on factors such as the species concerned, local costs, and the cost of competing technologies. However, optimizing rearing for numbers without regard to quality may compromise the effectiveness of the SIT. In the future, improvements in sex-separation technologies and in understanding the impact of microbiota on insect quality may lead to significant improvements in both rearing efficiency and quality. The list of target pest species for which mass-rearing systems have been, or are being, developed continues to expand.

1. INTRODUCTION

The sterile insect technique (SIT) depends upon inducing a high proportion of sterile matings in a natural population that reduces reproduction to a level below population maintenance. Therefore, the production of insects, in sufficient number and of adequate quality to achieve this aim, is one of the principal requirements for the successful application of the technique. Further, since the integration of the SIT into an area-wide integrated pest management (AW-IPM) programme competes economically with other control techniques, the production of insects must be timely and cost-effective. Large numbers of insects are required to integrate the SIT into AW-IPM programmes, and therefore it is possible to take advantage of economies-of-scale in the rearing.

There are numerous published accounts of the rearing of many insect species, including general reviews (Smith 1966; King and Leppla 1984; Singh and Moore 1985; Anderson and Leppla 1992; Ochieng'-Odero 1994a; Nordlund 1999; Schneider 2009; Cohen 2015; Beukeboom 2017). The details of specific rearing systems used by the various ongoing SIT projects are described in the published literature. Some key publications for the main SIT pest target groups are:

- *Moths*: Zethner (1980), Stewart (1984), Davis (2009), Dyck (2010), Carpenter and Hight (2012), Xsit (2018), Boersma (2021),
- *Screwworms*: Brown (1984), Mahon and Ahmad (2000), Scott et al. (2017), USDA/APHIS (2017),
- *Fruit flies*: Schwarz et al. (1985), Vargas (1989), Nakamori et al. (1992), Yamagishi and Kakinohana (2000), Cáceres et al. (2014),
- *Tsetse flies*: Feldmann (1994), Gooding et al. (1997), Aksoy (2005), FAO/IAEA (2006),
- *Mosquitoes*: Gerberg et al. (1994), Balestrino et al. (2014); Carvalho et al. (2014), Zheng et al. (2015a, b), FAO/IAEA (2017a, b, 2018a), Mamai et al. (2017a, 2018), Lees et al. (this volume), and
- *Weevils*: Yamaguchi et al. (2006), Shimizu et al. (2007).

Insects are reared for many reasons — bioassays, physiological research, rearing parasitoids, postharvest treatment testing, etc. (Singh and Ashby 1985), where rearing is rarely an end in itself. For these purposes, the cost of rearing is not critical,

e.g. the diets tend to be all inclusive, rather than minimal, and once a diet is developed that is able to maintain an adequate colony, little or no further work is done on it.

For the SIT, a rather different approach is needed, with due attention being paid to all the factors affecting quality, fecundity, and cost. Even though Singh (1985) listed more than 1300 species that have been reared on artificial diet in the laboratory for part or all of their life cycle, relatively few species have been mass-reared for the SIT (IDIDAS 2019). The details of the rearing protocol for any one species will not be discussed here, but examples to illustrate key points and issues common to the successful mass-rearing for the SIT will be given.

2. ECONOMICS

Mumford (this volume) discusses the economics of the SIT. However, that discussion focuses on benefit/cost analyses of overall programmes, and rearing economics appear only as a component of overall cost.

One of the main characteristics that distinguishes rearing for the SIT from other insect rearing is scale, e.g. the El Pino factory in Guatemala has the capacity to produce more than 2000 million sterile male Mediterranean fruit flies *Ceratitis capitata* (Wiedemann) per week (Figs. 1, 2).

Figure 1. Mediterranean fruit fly production and sterilization facility, El Pino, Guatemala (2015). Recycled/processed water from the facility is retained in a pond for the production of fish. (Photo from P. Rendón, reproduced with permission.)

Scale brings with it problems of labour supply, automation, and diet supply, which are dealt with later in this chapter, but there is also an issue of the relative efficiency and economics of scale. In general, cost per unit reduces as scale increases, and this can be seen in the efficiency of the Guatemala facility (Hendrichs et al. 2002). At the same time, if rearing is optimized for numbers without regard to quality, there is a risk of reduced quality (Parker, Vreysen et al., this volume). The scale at which a particular programme becomes cost effective will depend on the species involved and the cost and efficiency of alternate means of control.

Figure 2. Mass-rearing the Mediterranean fruit fly at the El Pino facility, Guatemala. Upper left: Eggs treated in a hot-water bath to kill female embryos of the temperature-sensitive lethal sexing strain; Lower left: Rearing larvae in trays, showing hanging plastic net sheets to redirect jumping mature larvae to the collection pan below; Upper right: Maturing pupae in trays stacked on trolleys; Lower right: Vertical cages for adult emergence, feeding, and egg oviposition and collection. (Photos from C. Cáceres, reproduced with permission.)

Unfortunately, few published data are available on the actual cost of rearing, separate from whole programme costs (IAEA 2008). The figures that are available indicate that costs have fallen dramatically, but the figures derive from different situations that are not directly comparable, and most of the change is attributable to improvements in rearing technology, rather than scale. The cost of male Mediterranean fruit fly pupae has been reduced to less than USD 300 per million in the Guatemala facility, but this cost depends on the utilization efficiency of the available capacity (Fig. 3) (Enkerlin 2003), indicating that utilization efficiency is at least as important as scale per se. Caceres et al. (2004) compared mass-rearing costs of Mediterranean fruit fly sexing and non-sexing strains; here the different characteristics of the *tsl* sexing strain lead to a small increase in rearing costs (which may be reversed with future developments), but significantly reduced post-production programme costs.

In Tanzania, with increased production, the production cost of the tsetse fly *Glossina austeni* Newstead was reduced from about USD 1 per male insect to less than USD 0.10; again, however, this is largely due to changes in procedures. The same applies to mass-rearing equipment. For example, innovations in mosquito mass-rearing techniques, including development of a low-cost adult-holding cage, resulted in a 10-fold cheaper cage (Maïga et al. 2019). Manufacturing the new mass-rearing cage locally can significantly reduce the initial investment in equipment. Also, improvements have been made in larval diets to reduce the cost 40–90% in *Anopheles arabiensis* Patton (Bimbilé Somda et al. 2017), and up to 80% in *Aedes* sp. (Bimbilé Somda et al. 2019; FAO/IAEA 2020).

Figure 3. Variation in Mediterranean fruit fly production cost (USD) with capacity utilization at El Pino, Guatemala. (Figure adapted from Vollmerhausen 2001.)

3. FACILITY DESIGN AND LOCATION

Facility design is a critical aspect of the rearing process (FAO/IAEA 2004, 2019b; IAEA 2008; Co 2019; NEA 2019). Poor design will lead to inefficient utilization of space and energy, increased problems with contamination, and increased risk of escape of fertile insects. Leppla and Ashley (1978), Griffin (1984), Fisher and Leppla (1985), and Fisher (2009) discuss general facility design. Specific aspects of biosecurity are discussed in USDA/APHIS/PPQ (1995), Kahn and Mathur (1999), Leppla and Eden (1999), and ACME (2003). Harrell et al. (1979), Owens (1984), Wolf (1984), Goodenough and Parnell (1985), Oborny (1998), and Schneider (2009) discuss environmental control. Tween (1987) discusses a modular approach to constructing the mass-rearing facility that has been adopted in Guatemala for the Mediterranean fruit fly; this is expanded in Cáceres et al. (2012). The modular approach has the advantage of simplifying design and expansion, but it also means that there is little economy from increased scale as each additional module costs the same as previous ones, the only saving coming from the common areas. However, it has the advantage of allowing the facility to be easily scaled to the required size, so as to maintain the utilization efficiency (Fig. 1); if demand falls, complete modules can be closed without affecting production in the remaining modules, or converted to rearing another insect.

The criteria for determining the optimum location for a mass-rearing facility must take several factors into account, both technical (Phillimore 2002; FAO/IAEA 2004) and managerial (Dyck, Reyes Flores et al., this volume). The principal factors, not in order of priority, are:

- Logistical access – ease of delivery of rearing supplies and equipment,
- Geological stability – earthquake risk, hurricanes, flooding, etc.,
- Political stability,
- Acceptance of the facility by the local community,
- Local government requirements or restrictions,
- Access to water and utilities, reliability of supplies,
- Construction and maintenance costs,
- Availability of support and repair services,
- Labour costs and availability,
- Waste disposal,
- Access to a suitable airport for rapid delivery of insects,
- Distance from release area,
- Quarantine considerations – can the insect survive in the surroundings?
- Proposed progression in case eradication is the objective – will the facility become stranded behind the eradication front?

The relative importance of a given factor will depend on the specific programme, and on factors such as labour costs and the degree of automation utilized. For highly sophisticated systems, access to support and maintenance for the equipment may be critical, as may electricity supply reliability, but for a less automated system these may be less important. Some of the factors can be accommodated within the programme itself, e.g. installing independent generation capacity and a water supply. Even though not always possible, locating the facility in an area where the insect

cannot survive and establish, perhaps due to desert conditions or cold winters, greatly eases the quarantine considerations, and reduces costs. The problem of being stranded behind the eradication front might be addressed by developing a relocatable, containerized rearing system.

4. ESCAPES AND ENVIRONMENTAL CONCERNS

A problem unique to the SIT is that the pest insect itself is being reared. For other large-scale rearing, e.g. classical or augmentative biological control, the reared insect is not the pest itself, so any escape from the rearing process is unlikely to pose a threat. (An exception is where the pest must be reared as a host for a parasitoid or predator, but living hosts are increasingly being replaced by factitious hosts or artificial diets). However, when the pest is being reared, any escape of fertile material poses a risk. Usually, the rearing is done in an area where the pest is already present, but if an eradication programme is successful, the rearing facility can become stranded behind the eradication front and poses a substantial reinfestation risk. This happened to both the Mexican facility producing the New World screwworm *Cochliomyia hominivorax* (Coquerel) and the Japanese facility producing the melon fly *Zeugodacus cucurbitae* (Coquillett). Stringent containment procedures are required (see references in section 3.), usually coupled with preventive sterile insect releases and other control measures in the vicinity of the rearing facility. Following screwworm eradication in the country, the screwworm facility in Mexico operated successfully for many years (although it was eventually replaced by a new facility in Panama), employing a combination of stringent security, containment, and prophylactic sterile-male releases. An alternative is to site the facility in an area where the insect cannot, due to local environmental conditions, establish a self-sustaining population, e.g. the facility constructed in Addis Ababa, Ethiopia, to rear the tsetse fly *Glossina pallidipes* Austen. In a mosquito-rearing facility, the risk of free-flyers increases with the scale; various tools such as light, odour, and gravid traps are commonly used to reduce the number of escaped mosquitoes (Lees et al., this volume; Vreysen, this volume).

The mass-rearing process for the SIT potentially poses some environmental problems in relation to waste disposal, including preventing the accidental escape of fertile insects with the spent diet and wastewater. These waste products must be treated to ensure that no living insects in any stage remain — for the diet by steam treatment or extrusion, and for wastewater by filtering, heat treatment or their combination with biological processes. Diets should be readily biodegradable to reduce environmental concern over waste disposal, or even to allow their re-utilization for other purposes, such as feeding fish or livestock (Fig. 1). Some of the bulking agents used in diets do not readily degrade, and these should be avoided, not least because they can lead to significant waste disposal charges (Chaudhury and Alvarez 1999). Facilities are also increasingly being required to install costly wastewater treatment plants. A recent study demonstrated the potential for using recycled larval-rearing water to supplement clean dechlorinated water when rearing *Anopheles arabiensis* (Mamai et al. 2017b).

Probably the biggest environmental concern comes from the sterilization process, which involves a radioactive source. Standard procedures for the use and eventual disposal of such sources are available and, if followed, minimize the risk (IAEA 2005). The increasing tendency to replace isotopic sources with X-ray systems greatly reduces the risks. Sterilization itself is discussed by Bakri et al. (this volume).

Insect mass-rearing can pose a significant health hazard through inhalant and contact allergies (Wirtz 1984; Wolf 1985; Bellas 1990; Kfir 1994; Myers and Barnard 2002; Reinecke 2009). Allergic reactions to mould spores, mites, and pheromones also occur. Some moths have urticating wing scales or hairs that can cause skin rashes and irritations in eyes and lungs (Moraru and Goddard II 2019). Preventing allergic reactions involves recognition and documentation of the problem (Wirtz 1980), and correction of the problem through appropriate air-handling and filtering (Owens 1984; Wolf 1984; Froehlich 1995), coupled with protective clothing and filter masks or respirators. The environmental conditions in the rearing facility may also be changed by manipulation of the diet (Vargas et al. 1984). In addition to the health hazard caused by spores and mites, they impact the rearing directly by reducing diet quality or causing disease in the insects (see sections 6., 8.4.) (Abd-Alla et al., this volume).

5. STRAIN MANAGEMENT

Strain management ensures that a strain continues to perform the function required of it, i.e. it survives under field conditions and remains sexually compatible with wild insects, and does not gradually deviate from wild behaviour. The strain must also maintain fecundity, and potential problems with contaminant organisms must be suppressed or eliminated. Fisher (1984), Schwalbe and Forrester (1984), Singh and Ashby (1985), and Caprio (2009) discussed strain management.

One of the most common concerns is the genetic diversity (heterozygosity) of the strain; this can be an important consideration during colony establishment. The strain must be colonized with a sufficient number of individuals from a wide genetic background. There has been much discussion, with a wide divergence of opinion, as to how many are sufficient — from many thousands to just a few tens or hundreds of females (Mackauer 1972, 1976 for parasitic wasps; Bartlett 1985 and Nunney 2002 for the SIT). It is generally agreed that the size of the founder population should depend on the degree of heterozygosity of the wild population. Usually it is stated that the founder material should come from a wide geographic range, but this is not necessarily beneficial; crossing strains from different geographic locations can break up adaptive gene combinations and render the strain less fit than the parents (Mackauer 1976). Azrag et al. (2016) compared the genetic diversity of an advanced generation of an *An. arabiensis* colony population with the field population from which the colony was derived. They found that using a small number of mosquitoes to establish the colony significantly reduced the total number of alleles, the numbers of rare and private alleles, and the fractions of heterozygote individuals at all the loci; this highlighted the need for broad sampling when colonizing a mosquito population (Benedict et al. 2009).

Individual fecundity will also influence founder numbers. In a slow-breeding group, such as tsetse flies, each individual has to be carefully nurtured, and no one individual's or small group's progeny can dominate the next generation. The logistics of collection also play a major role in how the field population is sampled.

Insects newly collected from the field rarely thrive in the laboratory, and the first few generations usually suffer high mortality, with the colony stabilizing after about five generations (Bartlett 1984). This process involves the rapid selection of individuals better adapted to the laboratory rearing conditions (Ochieng'-Odero 1994b), resulting in a rapid decline in heterozygosity. There is considerable concern that these changes will result in insects significantly different from the wild population, and therefore non-competitive, although as yet it has not been possible to show unequivocally that a reduction in heterozygosity per se leads to a reduction in competitiveness. Leppla et al. (1983) showed that this adaptation process was not influenced by gradually introducing mass-rearing conditions.

Adverse changes resulting from long-term mass-rearing are not uncommon, with the development of strains lacking the necessary courtship behaviour and responses to pheromones, predator avoidance, host odours, environmental cues, flight range, and even vision (Boller 1972; Miyatake 1998; Cayol et al. 2002; Mudavanhu et al. 2017; Parker, Vreysen et al., this volume). During long-term mass-rearing, due to the accumulation of random mutations, heterozygosity may gradually be regained (Bartlett 1984), but the newly acquired heterozygosity will not match that of the field population. Heterozygosity can also be encouraged deliberately (Joslyn 1984). To minimize selective processes on colonized mosquito populations, the induction of hybrid vigour by crossing strains of different origins (Craig 1964; Seawright et al. 1975; Ekechukwu et al. 2015) or a regular periodic replacement of existing colonies with wild stocks (especially males) obtained directly from the field (Dyck 2010; FAO/IAEA 2017a, 2018a), have been proposed or sometimes executed (Whitten and Foster 1975; Hofmann 1985; Saul and McCombs 1993; Parker, Vreysen et al., this volume).

Potential changes in competitiveness during mass-rearing are best detected by careful quality-control monitoring (FAO/IAEA/USDA 2019). A range of parameters is monitored routinely, including mating competitiveness and flight ability (Parker, Vreysen et al., this volume). If adverse changes are observed, it may be possible to deliberately select for desirable characteristics (Collins 1984; McInnis et al. 2002; Lommen et al. 2017; Sánchez-Rosario et al. 2017), although there are some dangers associated with this approach.

A recent development in mass-rearing the Mediterranean fruit fly has a potential application to colony management in almost any insect-rearing programme. The concept, called the filter rearing system (FRS), involves maintaining a small colony at a low density, or even under semi-natural conditions, and therefore assumedly a low-selection pressure (Fig. 4) (Cáceres et al. 2000; Fisher and Cáceres 2000; Hendrichs and Robinson, this volume). Surplus insects from this low-density mother stock or clean stream are fed into a high-density amplification chain, leading up to the final release numbers. The important feature is that no individuals are ever fed from the amplification stages back to the mother stock. The low-density rearing conditions of the filter can be supplemented with any further conditions deemed desirable, e.g. host plant, predators, mating competition or pheromone response, and

non-performing individuals eliminated. Any undesirable traits selected for in the high-density amplification stages have only three or four generations to accumulate before release, and do not affect the mother stock. A further advantage is that, if it is desired to replace the strain with a new one, the new mother stock can be set up in parallel with the old one, and amplification easily switched from one to the other. Filter rearing is similar to the concept used by Bigler (1986) to rear *Trichogramma maidis* Pintureau and Voegelé.

Figure 4. Continuous filter rearing system for producing Mediterranean fruit fly sterile males in Guatemala. (Figure adapted from Cáceres et al. 2000.)

6. PRODUCTION, PROCESS, AND PRODUCT CONTROL

The concept of quality control can be divided into three areas: production control (monitoring all rearing operations in terms of personnel, materials, equipment, schedules, environment, etc.), process control (sampling immature insect stages to predict quality and determine sources of variability), and product control (both at the output from a rearing facility and in the field), according to the normal industrial definitions (Leppä 1994). All three aspects are equally important in quality control, but most work has been done on product quality control (FAO/IAEA/USDA 2019; Parker, Vreysen et al., this volume). Field quality control is a particularly neglected area (Vreysen, this volume).

In general, methods of rearing for the SIT are developed from those used to rear insects for other purposes, but on a much larger scale. The techniques are similar, but the issues of quality control require a different approach. The larger scale means larger rearing facilities, and for larger facilities production control becomes critical and potentially more difficult. There are also greater opportunities for automation, reducing labour costs, variability, and the likelihood of microbial contamination from the staff employed in the facility (Abd-Alla et al., this volume). Environmental control systems are very important, and their design must take into account the amount of insect biomass producing heat (Oborny 1998). These are also amenable to increased automation, with networked monitoring of temperature, humidity, and light as is done in the codling moth *Cydia pomonella* (L.) rearing facility in Osoyoos, Canada (Dyck 2010). In an interesting approach to process control, air space volatiles were monitored for changes that would indicate changes in the rearing parameters (Hedin et al. 1975).

The specific nature of the SIT requires that the product, i.e. reared insects, mate with the wild population, and mating behaviour tests are critical (Parker, Vreysen et al., this volume). Several of the techniques used to measure these behaviours under semi-natural conditions in tephritid fruit flies (FAO/IAEA/USDA 2019) have been adapted for tsetse flies (Mutika et al. 2001). However, monitoring itself does not correct rearing problems. Each rearing facility should develop standard operating procedures (SOPs) for rearing operations, quality-control operations, and finally responses to adverse quality-control findings (FAO/IAEA 2018b).

Effective data management is a vital component to allow managers of large-scale mass-rearing to take appropriate and timely decisions (FAO/IAEA 2018b). Akey et al. (1984) reviewed data processing, and modern computer systems have further simplified data collection and analysis. As rearing becomes commercialized, customers will require up-to-date information on insect status and quality control, and this information could be made available via the Internet.

Finally, a factor not unique to the SIT, but more prominent with increased centralization of rearing, is the issue of transboundary shipment. To date, there is no explicit regulatory framework for the transboundary shipment of sterile insects, but this issue is currently being addressed (Enkerlin and Quinlan 2004; Dowell et al., this volume; Dyck, Reyes Flores et al., this volume). In this context, the existence and careful documentation of a comprehensive quality-control system will be important (FAO/IAEA/USDA 2019).

7. AUTOMATION OF REARING

The scale of rearing for the SIT naturally lends itself to some degree of automation. Rearing systems vary greatly in their sophistication, from largely manual (tsetse fly (IAEA 2003), New World screwworm (Scott et al. 2017)) to highly sophisticated (pink bollworm, melon fly) systems. The balance between labour and automation depends on many factors, but the chief one is the cost of labour. In areas with low-labour costs, the drive towards automation will be reduced, but in high-wage areas, e.g. Japan, automation is essential to reduce costs (Nakamori et al. 1992). Other reasons to automate include: (1) reduction in human error, with increased product performance and consistency, (2) reduction in microbial contamination from personnel, and (3) increased space utilization efficiency, resulting in lower costs — for building and for energy for environmental control (Cáceres et al. 2012).

Another aspect of automation is in climate-control systems. Air-handling is essential to control temperature and humidity (Schneider 2009), reduce airborne particulates and microbial contamination of the colony, and reduce medical problems of the staff (Reinecke 2009). Klassen (1978), Sikorowski et al. (1983), Harrell and Gantt (1984), Opiyo et al. (1999, 2000), Smith (1999), Smith and Nordlund (1999), Maïga et al. (2016, 2017), and Mamai et al. (2019) reviewed aspects of mass-rearing automation. For almost all stages of the process, descriptions of automated systems are available — egg collection (Leppla et al. 1974; Carlyle et al. 1975; Pearson et al. 2002), diet preparation and dispensing (Grisdale 1973; Gantt and King 1981; Miller et al. 1996), larval holding and pupal harvesting (Hartley et al. 1982), and environmental-control systems (Oborny 1998; Peng and Ohura 2000). Automation in mosquito mass-rearing is covered in more detail in Lees et al. (this volume).

8. DIET

Diet is probably the single most important component of rearing and, with labour, constitutes the main cost. Therefore, it is in the interest of insect-rearing programmes to improve the performance or reduce the cost of the diet. A balance has to be achieved between cost and performance of the insects; in the long run, a cheap diet that produces less competitive insects may prove more expensive. Chaudhury (2009) and Cohen (2015) reviewed all aspects of nutrition, feeding, and diet development.

Diets for many insects have been described in the literature (Smith 1966; King and Leppla 1984; Singh and Moore 1985; Gerberg et al. 1994; Ochieng'-Odero 1994a; Morales-Ramos et al. 2014; Skoda et al. 2014; Bimbilé Somda et al. 2017; FAO/IAEA 2017a, b, 2019a; Moadeli et al. 2017), with a gradual progression from natural-host materials towards synthetic and defined diets (Singh 1984; Moore 1985; Shimoji and Yamagishi 2004). A natural-host diet is limited by the availability of the host, which may be seasonal or limited in distribution, and variable in quality. It tends to be expensive, but should provide a complete diet and avoid changes in host-location behaviour. Semi-synthetic, synthetic, and defined diets offer the convenience of shelf storage and consistent product, but risk being deficient in one

or more factors. Often natural-host material needs to be incorporated into the diet for initial colonization, but then can be removed gradually as the colony adapts. Generalist herbivore insects tend to be the easiest to feed, with specialist herbivores, predators, and parasites being more difficult. Singh (1985) worked on a range of diets suitable for several to many species, even across different orders. However, even though general diets are unlikely to provide optimum nutrition and cost, they do act as a good starting point for developing diets for newly colonized species.

Future diet development will concentrate on utilization efficiency, ease of storage, cost, and availability (Aceituno-Medina et al. 2020). Defined diets may become important, but the highly refined ingredients may be expensive, and thus semi-defined diets utilizing cheaper local raw materials are more likely to be useful.

Research on fruit flies is investigating liquid diets, which increase utilization efficiency and ease disposal problems, and offer the possibility of recycling the diet by removing waste products and replacing only the nutrients that have been consumed (Fay and Wornoayporn 2002; Chang et al. 2004, 2006). Insects such as the yellow mealworm *Tenebrio molitor* L., house fly *Musca domestica* L., and black soldier fly *Hermetia illucens* (L.) are under investigation for their potential to be used as feed for mosquitoes (Bimbilé Somda et al. 2019). Nutrigenomics offers a powerful method for determining if specific diet components are deficient or in excess (Coudron et al. 2006).

8.1. Diet Cost

The first step in reducing the cost of a diet, which was not designed specifically for the species, is to remove unnecessary components. The next stage is to identify local agricultural products and industrial by-products (e.g. brewer's yeast, sugar cane bagasse) or standard commercial products that are cheap (Chaudhury et al. 1998, 2000; Cohen 2000; Shimoji and Yamagishi 2004), and provide the necessary nutrition and physical properties without adverse effects on the development, quality, and reproductive capacity of the insect (Gilles et al. 2011; Damiens et al. 2012, 2013; Khan et al. 2013; Yahouédo et al. 2014; Bimbilé Somda et al. 2017; Epopa et al. 2018). Often utilizing local components will also make the supply more secure.

Minor components of the diet frequently contribute a disproportionate amount to the cost. For example, many diets are gelled with agar, but agar is very expensive; several alternatives (as partial or complete replacements of agar) have been investigated (Leppla 1976; Spencer et al. 1976; Harris et al. 1984; Taylor et al. 1991; Honda et al. 1996; Chaudhury and Alvarez 1999). Such minor (by weight) components are important in controlling both the consistency and water retention of the diet; water is a crucial component that influences all stages of egg, larval, and pupal development.

Mechanical handling and processing of diet can also reduce costs, e.g. in the former pink bollworm *Pectinophora gossypiella* (Saunders) rearing facility in Phoenix, Arizona, USA, diet was processed and sterilized in a twin-screw extruder (Edwards et al. 1996; Miller et al. 1996). The application of agricultural-engineering

and food-processing techniques promises to produce significant further improvements (Cohen 2015).

8.2. Diet Quality

It is important to ensure the quality of diet ingredients before purchase or use, e.g. by monitoring the physical and chemical variability of the ingredients, bacterial load, and any insecticide residues, and using bioassays to assess its impact on insect development, production, and quality parameters. Poor quality control of diet ingredients is a major problem in mass-rearing, and therefore requires attention, including specifying chemical and biological assays that the ingredients must pass. In the end, a cheaper ingredient may in fact be more expensive due to frequent “crashes” in production caused by low-quality ingredients.

In AW-IPM programmes that integrate the release of sterilized insects, the availability of an irradiator means that diet components can easily be decontaminated. In rearing tsetse flies, the bacterial load of the blood diet (FAO/IAEA 2019a) is critical, and can be reduced through irradiation (Feldmann 1994). Bacterial contamination of wheat bran used in an uncooked diet for rearing the carob moth *Ectomyelois ceratoniae* (Zeller) can also be reduced by irradiation.

8.3. Additives to Diets

Additives to larval or adult diets can have a profound effect on the performance of insects (Augustinos et al., this volume; Dowell et al., this volume; Pereira et al., this volume). Supplementing boll weevil *Anthonomus grandis grandis* Boheman diet with beta-carotene increased dispersal and trap response (Reinecke 1991). In *An. arabiensis* mosquitoes, a vitamin mix (used as an additive) significantly decreased larval development time (Damiens et al. 2012).

Feeding methyl eugenol to adults of the oriental fruit fly *Bactrocera dorsalis* (Hendel) reduces the time to sexual maturity and the catch of sterile males in methyl-eugenol-baited traps (Shelly and Dewire 1994). Other minor components, that can be added to the adult diet or applied directly to modify the behaviour of released insects, are being identified (Papadopoulos et al. 2001; McInnis et al. 2002; Shelly et al. 2002; Lance and McInnis, this volume).

8.4. Micro-Organisms in the Diet

Control of disease in the colony, and of micro-organism contamination of the diet, are intimately linked (Abd-Alla et al., this volume). The identification and control of microbiological contaminants have been reviewed by Sikorowski (1983), Goodwin (1984), Sikorowski and Goodwin (1985), Sikorowski and Lawrence (1994), and Inglis and Sikorowski (2009a, b). Apart from immediate mortality, microbial contamination can lead to changes in development, body composition, and susceptibility to insecticides (Sikorowski and Goodwin 1985). Control begins with preventing infection by appropriate handling techniques and sterilization of

ingredients, as well as surface sterilization of eggs or pupae (Leppla et al. 1974). A wide range of antimicrobial compounds for insect diets has been tested (Gifawesen et al. 1975; Ludemann et al. 1979; Hartley et al. 1982; Funke 1983; Bathon 1977), but many are unsuitable, and none is suitable for all insect species. Alverson and Cohen (2002) found that some of the most common ones have a significant negative impact on rearing *Lygus hesperus* Knight. Other means of microbial control include irradiation and various forms of heat treatment.

Conversely, it is now recognized that many micro-organisms are important for many aspects of the biology of their hosts. It has been shown in fruit flies that probiotic application of *Enterobacter* sp. resulted in improvement of both pupal and adult productivity, as well as reduced rearing duration, particularly for males, without affecting pupal weight, sex ratio, male mating competitiveness, flight ability, and longevity under starvation (Augustinos et al. 2015; Yao et al. 2017; Cáceres et al. 2019; Stathopoulou et al. 2021). Kyritsis et al. (2017) described two bacterial isolates, an *Enterobacter* sp. (strain AA26) and a *Klebsiella oxytoca* strain, that were used as probiotics in larval and adult diets. These strains have been shown to be beneficial, affecting several aspects related to the rearing efficiency and biological quality of the Mediterranean fruit fly VIENNA 8^{D53+} genetic sexing strain, but other work did not find consistent benefits from probiotic diets (Niyazi 2004; Sacchetti et al. 2014), indicating that controlling the specific species and strains of micro-organisms in the diet and their concentrations will be important (Augustinos et al., this volume).

9. SEX SEPARATION

In the SIT, released sterile males mating with wild females produce the only sterilizing effect. If sterile females are also released, they can have (depending on the species) an additional positive effect by distracting wild fertile males and acting as a “sperm sink”. However, usually the simultaneous release of both sexes is less economical, and also less effective, than the release of only males, because there may be a tendency towards assortative mating (Robinson et al. 1999). In haematophagous disease vectors, the females are usually the vectors, and must be removed prior to release (Lees et al., this volume).

In most insects, the sexes can be separated on the basis of external morphology, but this may be possible only in the pupal or adult stages, and may be difficult to automate. For example, in programmes that release sterile male tsetse flies, teneral adult flies are usually hand-sorted in a chiller to separate the sexes, a very slow and laborious procedure. Research showed that a computer-based optical recognition system was too slow and too prone to error to be useful, but recent work on separating pupae according to sex by near-infrared imaging shows promise (Moran and Parker 2016). In many insects, e.g. some mosquitoes (Gerberg et al. 1994; Zacarés et al. 2018) and Lepidoptera, sexual dimorphism in size (apparent in the pupal stage) can be used to separate the sexes, but overlap in size (in some species) may render the sorting inefficient. In some insect groups, pupae show genitalia characters that identify the sex, but these are difficult to observe, require hand-sorting, and have not been automated. Spiking blood meals with ivermectin has

shown potential as a viable treatment to eliminate female *An. arabiensis* from laboratory colonies, but its practical use in a mass-rearing facility still needs to be tested (Yamada et al. 2013).

The sexes often show a variation in developmental rate, and this can sometimes be used to separate them. Female tsetse flies emerge first and, by manipulating temperature conditions during pupal development, sex separation based on the timing of adult emergence is possible (Opiyo et al. 1999, 2000); in some species the efficiency was more than 99%, and eliminated laborious hand-sorting work in a chiller. Protandry in mosquitoes results in males pupating/emerging before females, and larvae, male and female pupae can be separated using mechanical sexing tools (Focks 1980) or by using sieves of different mesh size. Automated systems using the difference in size between male and female pupae are currently under development to sort *Aedes* mosquitoes (Zacarés et al. 2018; Lees et al., this volume). Recent coordinated research (Bourtzis and Tu 2018) explored methods for sex separation in mosquitoes (Bellini et al. 2018; Kittayapong et al. 2018; Mashatola et al. 2018; Papathanos et al. 2018).

Various methods to separate the sexes, based on Mendelian genetics or engineered sex-linked mutations, have been developed (Robinson and Franz 1999; Robinson et al. 1999; Marec et al. 2005; Zepeda-Cisneros et al. 2014; Dandalo et al. 2018; Häcker and Schetelig 2018; Lebon et al. 2018). These systems, together with other genetic developments, are discussed by Franz et al. (this volume), Häcker et al. (this volume), and Lees et al. (this volume).

10. MARKING

To mark or not to mark sterile insects for release, that is the question. It is usually assumed that marking is essential for field monitoring of sterile to wild ratios so as to follow programme progress, but the hugely successful New World screwworm eradication programme (Klassen et al., this volume; Vargas-Terán et al., this volume) has never used any form of marking. Progress is monitored by measuring egg-hatch rates, and such a method may work for some of the other target insects as well (Vreysen, this volume). No one method of marking is universally applicable, and all may have negative effects on the insects (Dowell et al., this volume; Hendrichs and Robinson, this volume; Vreysen, this volume).

Methods of marking were reviewed by Hagler and Jackson (2001); the various individual marking systems, including numbering and coding systems, are clearly not appropriate for production levels of hundreds of millions per week. Methods appropriate to mass-rearing include dye marking (that can be observed directly or with a simple UV system), chemical marking that requires some form of instrumentation for detection, and genetic markers.

For any marking technique, quality control of the marking — detecting and rapidly correcting any failure of marking — is important (Enkerlin et al. 1996; Kohama et al. 2003). The misidentification of a released sterile insect as a fertile insect can have huge financial consequences for an AW-IPM eradication programme, justifying both the commitment of significant resources to, and great care in, the marking.

10.1. Dye Marking

Dye marking falls into two categories, internal dyes fed through the larval or adult diet, and external dyes. Internal dyes are usually oil-soluble; considerable testing of dyes has been done (Vail et al. 1966; Hendricks and Graham 1970; Graham and Mangum 1971; Hendricks 1971). It was found that a dye suitable for one species is not necessarily appropriate for even a closely related species. The ease of administering the dye in the diet makes this system very attractive, but the disadvantages are that the dyes can be toxic or cause behavioural or other changes (Schroeder et al. 1974) and may not persist in later stages; also, it is relatively difficult to identify a series of different markers. Nevertheless, the dye Calco Red has been used extensively for marking Lepidoptera, e.g. pink bollworm and codling moth. Rhodamine B has been shown to be a less expensive and a viable body-marking technique for *Aedes aegypti* (L.) without the negative side effects of traditional marking methods (Johnson et al. 2017).

Almost as extensively, external dye marking has frequently been used in AW-IPM programmes that release sterile insects. Usually this involves a fluorescent dye that is dusted or sprayed onto the insects (Chang 1946; Taft and Agee 1962; Stern and Mueller 1968; Schroeder and Mitchell 1981; Reinecke 1990; Enkerlin et al. 1996; Verhulst et al. 2013), but oil-soluble dyes have also been used for external marking (Steiner 1965; Schroeder and Mitchell 1981). The procedure is simple to apply; several different colours and dyes can be used. The impact of externally applied dyes on the behaviour or longevity of insects is variable (Nakata 2008; Reid and Reid 2008; Dickens and Brant 2014); it has been reported that excessive dye may reduce the response of codling moth males to calling females (Logan and Proverbs 1975). There is evidence that reducing the quantity of dye used can significantly increase survival and quality in fruit flies. The disadvantages of using external dyes are that an additional processing step is involved, the dyes may affect insect quality, the marker may not be as reliable as an internal one, and the dye dusts can pose a health hazard to staff.

10.2. Elemental Markers

An alternative to dye marking is using elemental markers (reviewed by Akey 1991 and Akey et al. 1991). Three forms of detecting elemental marking utilize radioisotopes, neutron activation, or one of several forms of atomic spectroscopy (Akey and Burns 1991) or isotope ratio mass spectrometry (Heiling et al. 2006). Elemental fingerprinting may also be included here — detecting the ratios of unsupplemented elements that will vary between field populations and mass-reared insects (Hood-Nowotny et al. 2009). Due to environmental concerns, radioactive-isotope marking has fallen out of favour. Neutron activation of rare elements is a very sensitive technique; in principle it is able to detect picogram quantities (Curtis et al. 1973; Hamann and Iwannek 1979), but the need for a fast-neutron source makes the technique extremely expensive and impractical.

Atomic absorption spectroscopy of stable isotopes offers a much more accessible technique (Akey 1991; Stimmann 1991; Van Steenwyk 1991; Fernandes et al. 1997;

Maciel-de-Freitas et al. 2004; Wilkins et al. 2007). Different forms of spectroscopy can be used to identify the marker with varying levels of sensitivity (Akey and Burns 1991). For a programme that releases sterile insects, the cost of false positives is potentially so high that the additional equipment and procedure may well be justified, particularly in the later stages of eradication, and elemental marking could provide a valuable second means of identification to back-up dye marking.

Hood-Nowotny et al. (2006) suggested that it was possible to use an isotopic label in adult *An. arabiensis*, and to detect it at an appropriate concentration up to 21 days post-emergence; however, the optimum labelling treatment would cost about USD 250 per million mosquitoes. Enrichment of semi-natural mosquito larval habitats with stable isotopes of nitrogen and carbon resulted in effective marking of *Anopheles* and *Aedes* mosquitoes colonizing these habitats (Opiyo et al. 2016).

10.3. Other Markers

An interesting development in chemical marking is the use of non-insect protein markers (Hagler and Cohen 1990; Hagler et al. 1992; Hagler and Miller 2002; Hagler 2004). The technique has been tested using rabbit IgG, fed in the diet or applied externally, and detected by sandwich enzyme-linked immunosorbent assay. The technique looks promising, requires only simple laboratory equipment, and rapid application should be possible. A big advantage is that the mark is completely invisible, and should have no biological effect on insects. Protein marking can be combined with dye marking to increase the marking efficacy (Irvin et al. 2012).

To distinguish released insects from wild ones, naturally occurring phenotypic mutations can be used in a similar manner to dyes, as long as the mutation is sufficiently rare in the wild population (Bartlett 1982). However, almost certainly, most mutations have some deleterious effect. For the SIT, the disadvantage is often not so great that their use is prevented, and a few such mutations have been investigated or used (Fay and Craig 1969; Schroeder and Mitchell 1981; Niyazi et al. 2005). The main problem with mutations is that, since they cannot be transferred between species by conventional genetics, they must be identified for each species to be marked.

Most mass-reared insect colonies have a limited genetic basis, resulting in limited genetic diversity. This can be exploited to distinguish colony insects from the target population, by identifying natural DNA markers specific to the colony or target insects. Mitochondrial DNA markers were used in South Africa to distinguish wild from released sterile insects (Barnes et al. 2004), but for identification this technique requires the use of polymerase chain reaction (PCR) amplification.

Once again, genetic engineering offers the prospect of new marking techniques (Häcker et al., this volume; Hendrichs and Robinson, this volume). In principle, any transgenic insect carries an identifiable marker (the transgenic construct), but for identification this also may require PCR amplification. It would be easier to use a gene that encodes a visible product. At present, the most popular genes are green fluorescent protein (GFP) and its derivatives (Peloquin et al. 2000), and DsRed (Alphey 2002). Fluorescent markers can be made sperm-specific to enable the sperm to be identified in mated field females (Scolari et al. 2008). Such transformations, if

carefully constructed, should avoid most of the disadvantages of natural mutation markers.

11. STORAGE

Successful field operations using the SIT require a timely and predictable supply of sterile insects, and this can present logistical problems. There is usually a premium on the release of sterile insects at the beginning of the target population build-up, before the population level becomes too large, but colony rearing may be constrained by diapause or hibernation quiescence. Also, for a seasonal pest, to save on costs, the rearing must be reduced to a maintenance level during the winter, but this is an inefficient use of the facility. In an ideal situation, the rearing would be continuous, with some means to stockpile the insects over winter in preparation for release in the spring, e.g. onion maggot *Delia antiqua* (Meigen) (Loosjes 2000). For these reasons, the ability to store insects, and to manipulate quiescence or diapause, becomes very valuable (FAO/IAEA 2016). For shorter timescales, storage for a few days may be useful to synchronize insects for periodic release, and storage in a quiescent state for a period of hours may be desirable for delivery to the release site and for the release process itself. Leopold (1998, 2000) reviewed cold storage and cryopreservation of insects for each of these timescales.

Insects with an obligate or facultative diapause may be of better quality than non-diapause individuals (Bloem et al. 1997, 1998, 2000) and, assuming diapause termination can be controlled, form a convenient way of storing insects. Denlinger (2002) reviewed the regulation of diapause. Obligatory diapause in a one-generation-per-year species, e.g. western cherry fruit fly *Rhagoletis indifferens* Curran (Vankirk and Aliniaze 1982), may make continuous rearing impossible. The main aim is to find a means to induce and then break diapause early to permit the production of sterile insects in advance of the field population. The duration of induction, diapause, and breaking of diapause may last many months, and present a formidable obstacle to successful incorporation into the rearing system. The obligate duration of some of the cues may be circumvented by the application of hormones, and certain volatile organic solvents can influence the termination of diapause (FAO/IAEA 2016).

The exposure of insects to low temperature often results in damage. Denlinger and Lee (1998) as well as Sømme (1999) reviewed the physiology of cold damage. Below 0°C the main threat to an insect is ice formation, but a range of hysteresis proteins, cryoprotectants, and stress proteins, and the elimination or masking of nucleating proteins and bacteria in freeze-susceptible species, lower the supercooling temperature below that likely to be experienced. Without freezing, osmotic stress is minimized. In freeze-tolerant species, nucleating proteins induce rapid freezing at higher temperatures, and osmotic stress is countered mainly by cryoprotectants.

Diapausing insects often exhibit inherent cold tolerance. Also, in many non-diapause insects, it is possible to induce cold tolerance by exposing the insects to heat or less extreme cold before storage, producing so-called “rapid cold hardening” in a matter of minutes or hours (Lee et al. 1987; Denlinger et al. 1992; Rinehart et al.

2000; Chidawanyika and Terblanche 2011; Nyamukondiwa et al. 2013). Cold or heat shock induces the production of specific stress proteins, commonly called heat-shock proteins (HSPs), which among other effects are thought to prevent protein denaturation (Parsell and Lindquist 1993). The rapid production of HSPs makes them useful for short-term storage, shipment, and release, but their effect can be longer term, and can be re-induced by brief warming to higher storage temperatures (Chen and Denlinger 1992). In the future, it may be possible to genetically engineer desirable traits to enhance the storage potential of a mass-reared strain (Robinson and Franz 1999).

Finally, during colonization and rearing, insects are subject to selection pressure of varying intensity that can result in rapid genetic drift and loss of heterozygosity. Cryopreservation provides a method for long-term storage of genetic material with specific desirable traits, and the storage of strains where diapause or conventional cold storage is not possible (Leopold 1998, 2000; Rajamohan et al. 2003, 2014; Rajamohan and Leopold 2007). Where it is possible, cryopreservation may reduce the labour and cost of maintaining continuously many strains.

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