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Review: Improving our knowledge of male mosquito biology in relation to genetic control programmes

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ABSTRACT

The enormous burden placed on populations worldwide by mosquito-borne diseases, most notably malaria and dengue, is currently being tackled by the use of insecticides sprayed in residences or applied to bednets, and in the case of dengue vectors through reduction of larval breeding sites or larviciding with insecticides thereof. However, these methods are under threat from, amongst other issues, the development of insecticide resistance and the practical difficulty of maintaining long-term

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community-wide efforts. The sterile insect technique (SIT), whose success hinges on having a good understanding of the biology and behaviour of the male mosquito, is an additional weapon in the limited arsenal against mosquito vectors. The successful production and release of sterile males, which is the mechanism of population suppression by SIT, relies on the release of mass-reared sterile males able to confer sterility in the target population by mating with wild females. A five year Joint FAO/IAEA Coordinated Research Project brought together researchers from around the world to investigate the pre-mating conditions of male mosquitoes (physiology and behaviour, resource acquisition and allocation, and dispersal), the mosquito mating systems and the contribution of molecular or chemical approaches to the understanding of male mosquito mating behaviour. A summary of the existing knowledge and the main novel findings of this group is reviewed here, and further presented in the reviews and research articles that form this Acta Tropica special issue.

1. Introduction

Mosquito-borne diseases threaten the lives and livelihoods of millions of people worldwide (Townson et al., 2005). Malaria alone affects over 300 million Africans (World Health Organisation, 2012), disproportionately affects the poor (Barat et al., 2004), and exerts such a huge public health burden that it has been blamed for the continued underdevelopment of the continent as a whole (Guinovart et al., 2006; Sachs and Malaney, 2002). Its burden is now estimated at 45.6 million DALYs (disability-adjusted life years). Malaria has been identified as a key contributor to weak economic growth and investment in Africa because it experiences the most intense malaria transmission in the world (Beier et al., 1999; Hay et al., 2000). Most of sub-Saharan Africa suffers from stable endemic malaria because climatic conditions ideal for transmission coincide with the ranges of *Anopheles gambiae* s.s., the newly designated *Anopheles coluzzi*, *Anopheles arabiensis* and *Anopheles funestus*, the most efficient vector mosquitoes in the world (Beier et al., 1999; Coetzee et al., 2000; Craig et al., 1999). In eastern and southern Africa, the proportion of all deaths caused by malaria increased from 18% in the 1980s to 37% in the 1990s (Korenromp et al., 2003). It is commonplace in tropical Africa for more than half the population to be infected with *Plasmodium falciparum*, by far the most dangerous of the four *Plasmodium* species that infect humans (Beier et al., 1999).

The dengue virus, causative agent of dengue fever (DF) and dengue haemorrhagic fever (DHF) transmitted by *Aedes* vectors, is probably the fastest spreading mosquito-borne disease agent with an estimated 390 million (Bhatt et al., 2013) cases per year worldwide. With no vaccine or efficient treatment, control of the disease is dependent on the suppression of the vectors but until recently, there has been no promising solution for their sustainable control. The trend for dengue vector control in most tropical regions has shifted from relying solely on insecticides to an integrated approach involving biological control, source reduction and environmental management through community participation (Gubler, 2004; Tapia-Conyer et al., 2012). Several Southeast Asian countries have recently carried out integration of vector control approaches (e.g. Kittayapong et al., 2008; Nam et al., 2005; Therawiwat et al., 2005; van den Berg et al., 2007). Similar moves towards integrated vector management (IVM) have been made in Africa against malaria vectors (e.g. Caldas de Castro et al., 2004; Chanda et al., 2008).

Indoor residual spraying (IRS) and insecticide-treated bednets (ITNs) are currently advocated for reducing transmission of malaria in Africa (World Health Organisation, 2008), each based on the use of residual insecticides in the intra-domiciliary domain and targeting mosquito vectors, before or after host-feeding, respectively. However, both methods have limitations such as insecticide resistance (Coetzee and Koekemoer, 2013; Roberts and Andre, 1994; Zaim and Guillet, 2002), environmental or human health concerns (Liroff, 2000; Turusov et al., 2002) and difficulties in achieving socio-economic or cultural acceptance by communities (Adongo et al., 2005; Noor et al., 2007). Effective as these tools are, they are not sufficient on their own to eliminate the malaria burden from the most intensely endemic regions, notably sub-Saharan Africa (Molineaux and Gramiccia, 1980; Najera, 2001). An expansion of this limited arsenal of vector control tools, with new strategies that can reduce human exposure, the density of mosquito populations, or transmissibility of infection, is therefore needed (Hemingway, 2004), and should preferably be appropriate for use in an integrated fashion with IRS/ITNs (Beier et al., 2008; Matthews et al., 2009; Shiff, 2002). Recent developments include the genetic sterilisation of *Anopheles* sp. (Catteruccia et al., 2009), repressible dominant lethal systems in *Aedes aegypti* (Fu et al., 2010; Phuc et al., 2007) and *Aedes albopictus* (Labbé et al., 2012), and the utilisation of *Wolbachia* infections (Lepage and Bordenstein, 2013).

These developments have led to renewed interest in the potential of the sterile insect technique (SIT) for suppressing mosquito vectors (Oliva et al., 2014b). The remarkable success of area-wide programmes integrating the SIT against screwworm (Wyss, 2000), tsetse (OAU/BAR, 2000; PAAT, 2000), and fruit flies (Hendrichs et al., 1983) provides a basis for contemplating the prospects for SIT interventions for suppressing mosquito vectors. It is envisaged that SIT would be used under specific conditions as an adjunct to other technologies. This would conform to the World Health Organisation's current vector-borne disease control strategy, integrated vector management (World Health Organisation, 2008), that emphasises avoiding reliance on any single intervention approach (Koul et al., 2008; Vreysen et al., 2007).

Unlike females, male mosquitoes are not blood feeders and thus do not transmit disease, which makes them logical agents for genetic control. Recent developments in the use of sterile male releases has sparked greater interest (Calkins and Parker, 2005; Ferguson et al., 2005), particularly in *Anopheles* sp. (Howell and Knols, 2009). However, although female biology and behaviour have been studied intensively, relatively little is known about males, for example the specific factors that contribute to male reproductive success are virtually unknown (Ferguson et al., 2005). Nevertheless, the success of any genetic control programme will hinge on the degree to which mass-reared released males are able to confer sterility in the target population.

2. FAO/IAEA sponsored coordinated research project

A Coordinated Research Programme (CRP) was initiated by the FAO/IAEA with the title "Increasing our knowledge of male mosquito biology in relation to genetic control programmes", which comprised 21 researchers from 16 diverse countries (Bangladesh, Benin, Burkina Faso, Cuba, Denmark, Ghana, Sudan, Syrian Arab Republic, Trinidad and Tobago, France, French Polynesia, Italy, Sweden, United Kingdom, United States of America and South Africa) working to address key questions in relation to the biology, physiology and behaviour of male mosquitoes, answers