



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

Rosemary Susan Lees^{a,*,1}, Bart Knols^b, Romeo Bellini^c, Mark Q. Benedict^d, Ambicadutt Bheecarry^e, Hervé Christophe Bossin^f, Dave D. Chadee^g, Jacques Charlwood^h, Roch K. Dabiréⁱ, Luc Djogbenou^j, Alexander Egyir-Yawson^k, René Gato^l, Louis Clément Gouagna^m, Mo'awia Mukhtar Hassanⁿ, Shakil Ahmed Khan^o, Lizette L. Koekemoer^{p,q}, Guy Lemperiere^m, Nicholas C. Manoukis^r, Raimondas Mozuraitis^s, R. Jason Pitts^t, Frederic Simard^u, Jeremie R.L. Gilles^a

^a Insect Pest Control Laboratory, Joint FAO/IAEA Division of Nuclear Techniques in Food and Agriculture, FAO/IAEA Agriculture and Biotechnology Laboratories, International Atomic Energy Agency, Vienna, Austria

^b In2Care BV, Costerweg 5, 6702 AA, Wageningen, The Netherlands

^c Centro Agricoltura Ambiente, «G. Nicoli», Via Argini Nord 3351, 40014 Crevalcore, Italy

^d Polo d'Innovazione Genomica, Genetica e Biologia S.C.a.R.L., Edificio D, 4° Piano Polo Unico di Medicina Santa Maria della Misericordia, Loc. S. Andrea delle Fratte, 06132 Perugia, Italy

^e Vector Biology and Control Division, Ministry of Health and Quality of Life, F6, Ex-Government Quarters, Botanical Garden Street, Curepipe, Mauritius

^f Institut Louis Malarde, (ILM), Laboratoire de recherche en entomologie médicale, rue des Poilus Tahitiens, B.P. 30, Papeete, Tahiti, French Polynesia

^g University of the West Indies, Department of Life Sciences, St. Augustine, Trinidad and Tobago

^h DBL Institute for Health Research and Development, 1 D Jaergersborg Alle, 2920 Charlottenlund, Denmark

ⁱ Centre Muraz Organisation de coopération et de coordination pour la lutte contre les grandes endémies, 01 B.P. 153, Bobo-Dioulasso, Burkina Faso

^j Institut Régional de Santé Publique (LRSP), Université d'Abomey-Calavi (UAC), BP.384 Ouidah & 01 BP 918, Cotonou, Benin

^k Ghana Atomic Energy Commission (GAEC), Biotechnology and Nuclear Agriculture Research Institute, Legon, PO Box 80, Accra, Ghana

^l Instituto de Medicina Tropical Pedro Kourí, Mariano 13, Apartado 601, Havana, Cuba

^m Institut de Recherche pour le Développement (IRD), UMR 5290/224 MIVEGEC (Maladies Infectieuses et Vecteurs: Ecologie, Genétique, Evolution et Contrôle), Plateforme Technologique du Centre de Recherche et de Veille sur les maladies, Emergentes dans l'Océan Indien (CRVOI), 2, rue Maxime Riviere, 97 490 Sainte Clotilde, Ile de la Réunion, France

ⁿ Epidemiology Department, Tropical Medicine Research Institute, Khartoum PO Box 1304, Sudan

^o Bangladesh Atomic Energy Commission (BAEC), Atomic Energy Research Establishment (AERE); Institute of Food and Radiation Biology, Ganakbari, Savar, PO Box 3787, Dhaka 1344, Bangladesh

^p National Institute for Communicable Diseases (NICD), National Health Laboratory Service, Sandringham, Private Bag X4, 2131 Johannesburg, South Africa

^q The Wits Research Institute for Malaria, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

^r US Pacific Basin Agricultural Research Center, United States Department of Agriculture-Agricultural Research Service, Hilo, HI, USA

^s Department of Chemistry, Organic Chemistry, Teknikringen 36, Royal Institute of Technology, 10044 Stockholm, Sweden

^t Vanderbilt University, Department of Biological Sciences, 465 21st Ave. S., Nashville, TN 37232, USA

^u Institut de Recherche pour le Développement (IRD), UMR 5290/224 MIVEGEC (Maladies Infectieuses et Vecteurs: Ecologie, Genétique, Evolution et Contrôle), 911 Ave Agropolis, BP 64501, 34 394 Montpellier, France

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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

* Corresponding author.

E-mail addresses: rosmarysusanlees@gmail.com, r.lees@poloinnovazionegg.com (R.S. Lees), bart@in2care.org (B. Knols), rbellini@caa.it (R. Bellini), mqbenedict@yahoo.com (M.Q. Benedict), abheecarry.vbcd@mail.gov.mu (A. Bheecarry), hbossin@ilm.pf (H.C. Bossin), dave.chadee@sta.uwi.edu (D.D. Chadee), jdcharlwood@gmail.com (J. Charlwood), dabire_roch@hotmail.com (R.K. Dabiré), ldjogbenou22002@yahoo.fr (L. Djogbenou), egyiryawson@hotmail.com (A. Egyir-Yawson), rene@ipk.sld.cu (R. Gato), louis-clement.gouagna@ird.fr (L.C. Gouagna), moawia65@hotmail.com (M.M. Hassan), ibd@aitlbd.net (S.A. Khan), lizettek@nicd.ac.za (L.L. Koekemoer), guy.lempriere@ird.fr (G. Lemperiere), nicholas.manoukis@ars.usda.gov (N.C. Manoukis), raimis@kth.se (R. Mozuraitis), j.pitts@vanderbilt.edu (R.J. Pitts), frederic.simard@ird.fr (F. Simard), j.gilles@iaea.org (J.R.L. Gilles).

¹ Present address: Polo d'Innovazione Genomica, Genetica e Biologia S.C.a.R.L., Edificio D, 3 piano Polo Unico di Medicina 'Santa Maria della Misericordia', Loc. S. Andrea delle Fratte, 06132 Perugia, Italy.

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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.

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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

to which were expected to be crucial for the advancement of the application of the sterile insect technique (SIT) (Robinson et al., 2009) and other novel forms of mosquito control. The CRP served to bring together a large research consortium that through collaborative research and knowledge exchange (facilitated by international Research Coordination Meetings or RCMs) aimed to significantly enhance the development of successful mosquito control programmes. Participants met at four RCMs between 2008 and 2013 that were held in locations where active research into the SIT is being conducted (two initial meetings at the IAEA in Vienna, Austria) or applied (Bologna, Italy and Juazeiro, Brazil). These meetings helped to foster collaborative relationships that informed and enhanced the progress of the individual research efforts and of the group as a whole. The results of this CRP are presented in brief in this review, and the key findings and reviews resulting from the participants' efforts make up the remainder of this special issue. Substantial advances have been made in understanding the nutrition, courtship behaviour, mating biology and response to a range of stimuli in laboratory, semi-field and various natural settings of several key vector mosquito species, mainly *Ae. aegypti*, *Ae. albopictus*, *Aedes polynesiensis*, *An. gambiae* s.s., *An. arabiensis*, and *An. coluzzi* (Coetzee et al., 2013). It is hoped that this new information will be of value to those scientists and vector control specialists aiming to develop and apply a range of techniques to control mosquito populations, efforts which are increasingly and urgently needed.

3. Specific objectives of the CRP

The Overall Objective of the CRP was to assist Member States of the FAO/IAEA in achieving sustainable control of mosquito-transmitted diseases through development and integration of the SIT into area-wide programmes against major mosquito species, though the programme also provided an increased knowledge base also of value to those developing other methods of mosquito control. The specific objectives of the CRP (Table 1) were to advance the understanding of critical behavioural and ecological components of male mosquito biology so as to be capable of producing high quality and sexually competitive sterile males in mass-rearing facilities. The proposed implementation of mosquito SIT is aided by basic and applied research into field populations of adult male mosquitoes in order to establish the specific biological and behavioural determinants that contribute to their sexual competitiveness.

Any genetic control programme begins with the colonisation and mass rearing of males, followed by sterilisation, shipping, and finally release of these males into the target population. A previous CRP focussed on developing methods of mosquito mass rearing, leading to the point of release. As a logical extension, this CRP proposed to study factors following release that may have an impact on the success of a release programme by studying laboratory and field populations of adult male mosquitoes to establish the specific biological and behavioural determinants that contribute to male sexual competitiveness. We defined male competitiveness as the degree to which a released male is able to copulate with wild females in the field relative to the rate of wild males. The factors that contribute to this competitiveness are myriad and are determined by natural selection and environmental factors. Accordingly this CRP focussed on male physiology and sexual behaviour, male bionomics, and male responses to external cues. Considering the current absence of effective sampling methods for male mosquitoes and appropriate marking methods to study the fate of released males, research in these two areas was also included.

Publications resulting from investigations under each specific objective of the CRP are listed in Table 1. Further publications were produced by participants during the course of the CRP which did not directly address the specific objectives but which were

nonetheless valuable contributions to the field, addressing questions about species distribution (Djogbénou et al., 2010; Guillaumot et al., 2012; Marie and Bossin, 2013) and population surveillance (Albieri et al., 2010; Brown et al., 2011; Carrieri et al., 2011a, 2012; Hapairai et al., 2013a,b; Iyaloo et al., 2014; Mercer et al., 2012a,b). Alternative methods of controlling mosquitoes were proposed by de Oliveira Carvalho et al. (2014), and Bourtzis et al. (2014), and the requirement for new sex separation techniques is reviewed by Gilles et al. (2014).

4. Mosquito male pre-mating conditions

Data on mosquito male biology are a prerequisite for approaches to mosquito control that incorporate large-scale releases of sterile (or otherwise genetically modified) insects for population suppression or replacement. The ultimate objective of male mass-releases is to produce males that mate competitively with wild males. In order to determine the comparative biology and competitiveness of mass-reared released males, detailed information is needed about all events in the life of both wild and sterilised male mosquitoes that impact their sexual competitiveness. For example, rearing conditions will be important. To this end the group studied quality control parameters such as development and survival of larvae, adult longevity, flight ability and mating competitiveness. Studies examined the impact of larval feeding regimes (Damiens et al., 2012; Yahouédo et al., 2014; Puggioli et al., 2013), mass rearing systems (Balestrino et al., 2012), sex separation methods (Yamada et al., 2013), and alternative sterilisation methods (Gato et al., 2013, 2014) on laboratory-reared males compared to wild-caught or recently colonised males.

There is great interest in resource acquisition, allocation and use by males, and a need to identify ecologically relevant behavioural and physiological traits that shape male fitness in the field. It is important to know how to use this knowledge to improve competitiveness of mass-reared mosquitoes for release. Male mosquitoes feed on plant-derived substances rather than blood (Foster, 1995; Gary and Foster, 2004; Impoinvil et al., 2004; Yuval, 1992). Although the specific sources of these substances have been established for several New World aedine and culicine mosquitoes in a range of settings (de Meillon et al., 1967; Müller et al., 2010, 2011; Smith and Gadawski, 1994), where anophelines acquire their nutrients remains largely unknown. Where sources of nutrition can be identified in the field, release strategies can be tailored to optimise male performance. Protocols were therefore developed by members of the CRP to identify the main sources of energy for male anophelines in the field. Males were found to be able to select more nutritionally rewarding sugar sources, probably increasing their mating success (Gouagna et al., 2010, 2014). Fitness of field and laboratory reared *An. gambiae*, *An. arabiensis* and *Ae. albopictus* was assessed when males were fed on various sugar sources (Dabiré, personal observation).

Empirical studies have shown that frequent sugar meals are significantly associated with reproductive success of male mosquitoes (Gary et al., 2009; Stone et al., 2009), particularly in anopheline species which mate in swarms, as one bout of swarming activity consumes ~50% of the energetic reserves available (Maiga et al., 2014; Yuval et al., 1994). The highly skewed sex ratio in swarms results in intense competition for the relatively few females. Some males mate several times, while most never mate at all (Bock et al., 1983; Reisen et al., 1982; Slooten and Lambert, 1984; Yuval et al., 1993). Participation in a swarm was shown to be predicated on a successful foraging bout during the preceding night (Yuval et al., 1994). Participants in the CRP also found that sugar feeding was associated with greater insemination rates in *Ae. aegypti* (Chadee, personal observation), and a large proportion of male Anophelines

Table 1

Specific objectives of the FAO/IAEA Coordinated Research Programme “Increasing our knowledge of male mosquito biology in relation to genetic control programmes”, divided into three key areas, and the publications resulting from this programme.

Main areas of activity	Specific objectives	Papers published by CRP participants
Mosquito male pre-mating conditions	How rearing conditions affect fitness of the males	Benedict et al. (2009), Hapairai et al. (2014), Maïga et al. (2014), Medici et al. (2011), Papathanos et al. (2009)
Male physiology and behaviour	Male nutrition in the field	Charlwood (2011), Charlwood et al. (2012), Gouagna et al. (2010), Gouagna et al. (2014), Howell and Knols (2009), Maïga (2011), Maïga et al. (2012), Ouedraogo (2008), Poueme (2008)
Resource acquisition and allocation	Develop purpose-specific trapping systems	Carrieri et al. (2011b), Hapairai et al. (2013b), Mercer et al. (2012a)
Male dispersal and sampling tools	Develop appropriate olfactometers and related guidelines to investigate species specific behaviours	None published to date
Mosquito mating systems	Develop release device systems for adults and pupae	Bellini et al. (2014)
	Determine the temporal and spatial characteristics of mating encounter sites of Aedine and Anopheline mosquitoes	Chambers et al. (2013), Chadee and Gilles (2014), Manoukis et al. (2014), Sawadogo et al. (2013b), Sawadogo et al. (2014)
	Investigate the behaviours involved in courtship	Assogba et al. (2014), Bellini et al. (2010b), Butail et al. (2012), Charlwood et al. (2011), Dabiré et al. (2013), Dabiré et al. (2014), Hassan et al. (2014), Manoukis et al. (2009), Sawadogo et al., 2013a Dahan and Koekemoer (2014), Oliva et al. (2014a), Sawadogo et al. (2013a)
	Copulation and insemination	None published to date
Contribution of molecular/chemical approaches to the understanding of male mosquito mating behaviour	Determine patterns of female remating, and how male performance affects this behaviour	None published to date
	Assessment of relative mating capacity and competitiveness	Bellini et al. (2013a), Bellini et al. (2013b), Chambers et al. (2011), Gato et al. (2013, 2014), Hassan et al., 2010, Kerampran (2012), Madakacherry et al. (2014), Munhenga et al. (2011), O'Connor et al. (2012), Sawadogo et al. (2013a)
	Extract and identify potential swarming/aggregation volatiles from mosquitoes	None published to date, though Pennetier et al. (2010) address auditory cues for species recognition and Pitts et al. (2014) review chemically-mediated behaviour of male mosquitoes
	Extract and identify volatiles from release-site plants as potential attractants for males	Eriksoon (2012)
Contribution of molecular/chemical approaches to the understanding of male mosquito mating behaviour	Extract and identify compounds in known feeding sources of nectar, fruit and perhaps honeydew for male mosquitoes. Use as a model for a dietary formulation for sterile males	None published to date
	Use olfactometers to test potential attractive volatile compounds using wild males versus mass-reared, irradiated males	Bernard (2012)
	Use PCR-based analysis of Y chromosome markers in <i>An. gambiae</i> to assess M and S molecular form distribution and male dispersal characteristics in Ghana	None published to date

collected in swarms in Burkina Faso had taken a sugar meal before swarming (Gouagna, personal observation). The nature of the available sugar source was found to affect survival, flight ability and mating competitiveness in *An. gambiae* s.s. (Maïga et al., 2012). A pupal release device providing access to sugar post-emergence was developed and tested in Italy (Bellini et al., 2014). Feeding increased mating competitiveness in both irradiated and fertile males released from this device.

It is imperative to know the size of natural target populations and the dispersal and survival of wild males prior to any release. This depends on the availability of efficient sampling tools, several of which were tested by CRP participants. Concrete block piles and tent traps were shown to catch male mosquitoes in Ghana (Egyir-Yawson, personal observation), and large pit resting shelters were found to be most effective in Sudan (Benedict, personal observation). Ovitrap surveillance data correlated well with other calculated indices when used to estimate seasonal population dynamics of *Ae. albopictus* in Italy (Bellini, personal observation), as did the use of BG-sentinel (BGS) and BG-mosquitito (BGM) traps (with BG-lure or carbon dioxide plus octenol) for *Ae. polynesiensis* in French Polynesia (Mercer et al., 2012a,b). These traps are therefore suitable replacements for human landing catches, the technique currently employed in French Polynesia.

Active dispersal, restricted in mosquitoes to the adult stage, is a critical issue for all living organisms, ensuring optimal genetic interchange and exploitation of habitat (Kennedy, 1975). Delivery of sterile males into the environment should be designed to ensure maximal interaction of the treated insects with the wild population, relying on fundamental knowledge of the natural dispersal dynamics and dispersal capability of released males. In addition, knowledge of dispersal of females will be required

to assess the significance of immigration of fertile insects from untreated areas. Information on dispersal capabilities will enable the programme to define the area to be treated with sterile males and to establish effective barriers against immigration of fertile males or females. Mark-recapture studies of several species have demonstrated movement ranging from a few hundred meters to 90 kilometres (Service, 1997), but nearly all previous studies have focused on female dispersal (Takken et al., 1998). During the course of this CRP, isotope marking was used to demonstrate dispersal of up to 1.5 km in *An. gambiae* and *Anopheles melas* males in Benin (Djogbenou, personal observation), but was considerably less among male *An. funestus* from Mozambique (Charlwood, 2011). Average dispersal of male *An. polynesiensis* was shown by MRR studies to be over 100 meters, depending on elevation (Mercer et al., 2012a,b). Marking methods based on *Wolbachia* were used to study the dispersal capacity of reared *Ae. albopictus* males in urban areas of Italy showing mean distance travelled was in the range of 97–212 m (Bellini et al., 2010a).

5. Mosquito mating systems

Mating systems encompass all of the ecological, behavioural and physiological attributes that lead to mate encounter, copulation, insemination and fertilisation. Many gaps remain in our understanding of mosquito mating systems. The research undertaken within the CRP aimed to better clarify these mating systems with the goal of establishing correlates to male success that can be applied to rearing, handling and release of mass reared mosquitoes in SIT and other release operations. *Anopheles* and *Aedes* species employ different strategies to encounter females. *Aedes* males, once sexually mature, are capable of mating at any time of day, though a

peak of mating activity occurs in the afternoon, respond to human host cues, and may encounter females outside or inside houses, as illustrated by field work conducted by participants of the CRP. *Ae. aegypti* mating was observed in Trinidad and Tobago to occur near larval sites and within houses with peaks of activity in the morning and afternoon (Chadee, personal observation). In contrast, *Ae. albopictus* mating was observed in Italy to mate in the late afternoon, in small swarms that formed close to the ground in shaded areas close to tree trunks, or as individual pairs in the vicinity of a blood meal host (Bellini, personal observation).

Mating in anophelines, in contrast, has historically been most commonly described in crepuscular swarms that form in response to prominent visual markers (Downes, 1969; Sullivan, 1981; Yuval et al., 1993). However, some anopheline species such as *Anopheles darlingi* are thought not to swarm (Lounibos et al., 1998), and others, including *An. gambiae*, may combine typical swarming behaviour with an alternative tactic, such as copulating at emergence, or near bloodmeal hosts or resting sites (Dao et al., 2008). For mass-reared males to succeed in their quest for virgin females, it is imperative that they show up at the right time and place, but determining when and where this is has proved difficult to study, as swarms are small and inconspicuous, occurring in conditions of low light (Charlwood et al., 2002a, 2003). Very little is thus known about how encounter sites are located, how sympatric pre-copulatory (isolation) mechanisms operate, and what cues are important. The location of species specific mating sites is perhaps the most efficient way of maintaining isolation between species or subspecies, and it is crucial that released males are able to locate and join swarms at the appropriate time to meet their conspecifics. Cues used for marker selection are important for swarm location, and if a 'super marker' could be created it could prove useful for male trap development.

Large and significant studies were conducted by participants of the CRP into the swarming and mating behaviour of natural populations of anopheline and aedine mosquitoes, with longitudinal surveys conducted between 2006 to 2012 in Burkina Faso (Sawadogo et al., 2014), Benin (Assogba et al., 2014), Ghana (Charlwood et al., 2011), Mozambique (Charlwood, 2011), La Réunion (Bossin, personal observation), Trinidad and Tobago (Chadee, personal observation) and Sudan (Hassan et al., 2014). A consistent need for swarm markers within and around human habitats, even if far from larval sites, was seen in all participant countries. In Benin swarms of members of the *An. gambiae* complex were seen to form over markers including wood piles, wells and pig feeders (Assogba et al., 2014), similar to those markers used by *An. arabiensis* in Burkina Faso (Dabiré et al., 2014). In Sudan *An. arabiensis* was observed to swarm near larval sites around irrigation channels (Hassan et al., 2014). Few mixed species or molecular form swarms were observed in Burkina Faso (Sawadogo et al., 2014), and swarms all formed between 1.5 and 4 m above the ground. Swarming in *An. gambiae* was confirmed by all studies to mainly occur at sunset, though a limited amount of swarming was observed in São Tomé and Príncipe (Charlwood et al., 2002b) with minor temporal segregation observed between *An. coluzzi* (formerly M form *An. gambiae*) and *An. gambiae* (formerly known as the S form) in Burkina Faso (Dabiré et al., 2013; Sawadogo et al., 2014).

The mechanics of copulation have been described in detail in the past (reviewed by Clements, 1999 and Howell and Knols, 2009), and an updated review of *Aedes* male reproduction is included in this special issue (Oliva et al., 2014a). Copulation in *Ae. albopictus* was observed to result in successful insemination in the majority of cases only if copulation lasted for more than 30 s (Oliva, personal communication). Sperm production and replenishment of sperm stocks over time was shown to be affected by irradiation at 70 Gy in *An. arabiensis* (Damiens et al., 2013); in 40 Gy pupal-irradiated *Ae. albopictus* males no difference in initial insemination attempts was

seen, though sperm replenishment was diminished (Oliva, personal communication).

In the mating arena the operational sex ratio (Emlen and Oring, 1977) of mosquitoes is highly skewed towards males (Yuval et al., 1993) so it is important to identify the characteristics that determine which males succeed in copulating, so that the performance of released sterile males can be better focussed and maximised. The relationships between size, age, nutrition and copulatory success in the field are not well understood, so efforts were made by CRP participants to elucidate the interactions. Male size and age influenced copulation success in *An. gambiae* in (Sawadogo et al., 2014) but not in *An. coluzzi* from Sao Tome (Charlwood et al., 2002a, b) nor in *Ae. aegypti*. No relationship was observed in Burkina Faso between proportion of *An. gambiae* males leaving in copula and swarm size (Charlwood et al., 2002a, b; Sawadogo et al., 2014), but a positive relationship with the number of females caught by trapping in the previous days was observed (Dabiré, personal observation).

The lifetime mating capacity and relative mating competitiveness of laboratory reared sterile males can be studied in comparison to those of wild fertile males in laboratory and semi-field experiments that compare the ability of each type of male to achieve copulation and insemination, or those that mimic the release of sterile males into a population. This latter form of experiment may take the form of simply adding a mixture of fertile and sterile males to females in a cage and determining their resulting fecundity/fertility, or a stable cage population may be established and the effect of sterile male 'releases' on the reproductive capacity or overall population of the cage determined relative to a control cage. All of these types of experiment were conducted by participants of the CRP during the course of the programme. Thus the relative competitiveness of field-collected and laboratory-reared, and irradiated and un-irradiated males was investigated in a range of species and settings: small and large laboratory cages as well as larger semi-field enclosures.

The relative competitiveness of field collected, laboratory reared, sterile and fertile males was investigated in *An. arabiensis* in South Africa (Munhenga et al., 2011), in *Ae. albopictus* in Italy (Bellini, personal observation), Austria (Madakacherry et al., 2014) and La Réunion (Oliva et al., 2012), in *A. polynesiensis* in French Polynesia (Chambers et al., 2011) and in *A. aegypti* in Trinidad and Tobago (Chadee, personal observation) and Cuba (Gato et al., 2013, 2014). Good mating compatibility was reported between colonised males and their wild, field-collected counterparts in several laboratory experiments. Male *Ae. albopictus* irradiated at 35 Gy as pupae were released into a semi-field cage in La Réunion at a 5:1 ratio produced a 50% reduction in egg hatch rate (Oliva et al., 2012), and male *Ae. aegypti* sterilised with thiotepa (6000 mg/L for 6 h) in a 5:1 ratio eliminated stable large cage populations (Gato et al., 2013, 2014). No significant reduction in the rate of copulation, insemination or number of eggs laid was observed in females mated to 40 Gy-irradiated male *Ae. albopictus* relative to those mated to un-irradiated males (Oliva, personal communication). *Ae. albopictus* males irradiated with 35 Gy as pupae were found to be more competitive at 1 than 5 days old when competing in a 1:1 ratio with fertile males in semi-field conditions in La Réunion (Oliva et al., 2012). The higher the male:female ratio the lower the competitiveness index of irradiated *Ae. albopictus* males in small and large laboratory cages and semi-field cages (Madakacherry et al., 2014). Marked, irradiated *A. arabiensis* males were seen to join natural swarms in Sudan, suggesting competitiveness (Damiens, personal observation). The removal of *An. arabiensis* females using blood meals spiked with dieldrin had an initial but not a long term impact on sperm production of remaining males (Yamada et al., 2013). Evidence of female remating was seen in *Ae. aegypti* and *Ae. albopictus* in the field (Boyer et al., 2012), which may have implications for the application of the SIT.

The functional significance of the presence of three spermathecae was investigated in *Ae. aegypti* and *Ae. albopictus* in the field, showing size differences and preferential filling between spermathecae (Chadee, personal observation). Ability of males to fill all spermathecae increased with their size in these species.

There is a need to introduce better definition of terms and improvements in methodological standardisation to support the design of future experiments and subsequent comparability of results. The extrapolation of laboratory and semi-field collected data to the real world also remains an important issue to be considered and possibly evaluated quantitatively.

6. Contribution of molecular and chemical approaches to the understanding of male mosquito mating behaviour

Availability of multiple mosquito genomes (Arensburger et al., 2010; Holt et al., 2002; Nene et al., 2007) has facilitated the identification of large families of receptors involved in peripheral volatile chemicals (e.g. Bohbot et al., 2007; Hill et al., 2002; Pelletier et al., 2010). The expression of mosquito odorant receptors (ORs) in heterologous cells has enabled the characterisation of odour ligands for a large number of receptors in multiple species (Bohbot and Dickens, 2009; Carey et al., 2010; Hallem et al., 2004; Wang et al., 2010). Like their mammalian counterparts, some receptors have been characterised as broadly tuned, or responding to multiple ligands, while others are very narrowly tuned to one or just a few odours. A few mosquito ORs, all of which respond to indolic compounds, known plant volatiles and oviposition cues (Bohbot et al., 2007, 2011; Hughes et al., 2010), are well conserved at the amino acid and functional levels (Bohbot et al., 2011; Hughes et al., 2010). Recently, insect repellents have been shown to inhibit the responses of mosquito ORs to their natural ligands (Bohbot and Dickens, 2010). Finally, a new class of chemoreceptors has been identified, the *An. gambiae* ionotropic receptor family (Ag1r). Expression patterns of ORs and Irs in antennae and maxillary palps have been examined in both sexes of *An. gambiae* (Iatrou and Biessmann, 2008). While the repertoire of expressed chemoreceptors largely overlaps between the sexes, the transcript levels differ significantly, where males show lower general expression of all receptors. This suggests that males may be sensitive to the same chemical compounds as females, but perhaps at lower thresholds. All of these studies open up new possibilities for the development of novel repellents or attractants that are specific to mosquito ORs. These could be included in integrated pest management programs as repellents that reduce human biting indices or attractants for baited traps that either reduce mosquito density and biting frequency or aid in mosquito surveillance. They may also support the provision of energetic substances to sterile males prior to release, help to create swarm marking sites for field investigation of courtship behaviour, or enable researchers to confer a mating advantage to sterile males.

The role of chemicals in the biology of mosquitoes was first explored by Rudolfs (1922), and the wide range of studies which has been carried out in insect chemical ecology has subsequently led to the use of semiochemicals in the control of agricultural and forestry pests. Clements' textbook on mosquitoes (1999) summarised the principles of olfaction, sensory reception and behaviour. Since then, odour-mediated host interactions have been widely investigated but only recently have studies on other behavioural aspects like mosquito–plant interactions been initiated. Understanding the chemical ecology of mosquitoes requires greater investigation of insect–host (attraction to humans or other vertebrates), insect–plant (attractants and repellents in host feeding of adults and larvae), insect–insect (chemical communication between adults), and insect–environment (attraction to oviposition

sites) interactions, using an interdisciplinary approach, including molecular biology, electrophysiology and analytical chemistry.

Little is known about the short-range interactions that lead to mosquito mating (courtship), or what behaviours are involved with species-specific mating, either in swarms or singly, but clearly they are likely to be vulnerable to selective pressures during colonisation where mating occurs in a limited space and highly homogeneous conditions. How to shape the mass rearing environment in order to maximise courtship behaviour and mating capacity remains largely unexplored. In the absence of spatial or temporal separation between species, pre-copulatory mechanisms in the form of contact pheromones are probably used to distinguish between species (Nijhout and Craig Jr., 1971). Released males must be able to compete with wild counterparts in terms of creating the correct olfactory, auditory or tactile cues and respond appropriately. Sex pheromones play a key role in the mating behaviour of many dipteran species, serving as a long-range attractant to bring males and females together and as a means of species identification. Clearly, if sex pheromones are produced in vector species, this would be of direct relevance to the likelihood of success of SIT, since attractant compounds would be valuable for trapping methods and may be useful in manipulating swarm formation. Also, differences, if any, between reared and sterilised males and their wild counterparts could be identified and work conducted to minimise its impact, or super-males produced by planning appropriate rearing condition.

It has been known for decades that male mosquitoes hear and respond to female flight tones by flying towards the source of the sound, and until recently it has been assumed that the only role of auditory cues in mating behaviour was for male location of females. A study on the flight-tone harmonics between tethered *An. coluzzi*, *An. gambiae* and *Ae. aegypti*, however, showed consistent frequency-matching between members of the same species, but not between heterospecifics (Pennetier et al., 2010). Male/female pairs harmonise their wingbeat frequencies when they are within ~10 cm of each other (Cator et al., 2009), a mechanism which may play a role in mate recognition, preventing hybridisation between incipient species (Pennetier et al., 2010). Swarm formation may involve a combination of visual and olfactory cues, though pheromones have yet to be shown to be present (Howell and Knols, 2009).

Against this backdrop, some investigation was conducted by CRP participants into the olfactory, tactile, auditory and visual cues involved in courtship. Stereoscopic video analysis of *An. gambiae* s.s. in Mali revealed swarms to be spherical with a higher density at the centre. The oscillatory movement of individual males was described that allows the creation of computer simulated swarms (Butail et al., 2013; Manoukis et al., 2009). Volatile compounds involved in the behaviour of both *An. arabiensis* and *Ae. albopictus* were identified from mosquitoes collected on La Réunion, and include octanal, nonanal, and 2-hydroxy-2-butanone (Bossin, personal observation). Amounts of detected octanal, nonanal, decanal, sulcaton, 3-hydroxy-2-butanone and 2,3-butanediol were shown to increase during swarming and/or aggregating in male *An. arabiensis* compared to control males and those collected before swarming (Mozuraitis, personal observation). Feeding larvae or adult mosquitoes with ¹³C labelled glucose showed incorporation in all three aldehydes, 2,3-butanediol, sulcaton, and 3-hydroxy-2-butanone, confirming their production by mosquito males. Many dipteran species have been shown previously to use cuticular hydrocarbons to detect conspecific individuals (Ferveur, 2005; Martin and Drijfhout, 2013), but this has not been fully explored in mosquitoes. Preliminary research by CRP participants to identify the cuticular hydrocarbons of *A. gambiae* s.l. indicates that the profile of components alters over the course of the mosquito's lifetime (Mozuraitis, personal observation). These compounds

have previously been shown to be altered during mating in both *An. gambiae* and *Ae. aegypti* (Polerstock et al., 2002) so they warrant further investigation.

7. Conclusion

Progress has been made by the participants of the Joint FAO/IAEA CRP into better understanding the male mosquito, but many answers are still to be found and many valuable avenues of research remain to be explored. It is hoped that this review and the special issue as a whole will be useful to readers in inspiring further research into the biology and behaviour of male mosquitoes in support of the successful application of the SIT and other vector control techniques.

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References

- Adongo, P.B., Kirkwood, B., Kendall, C., 2005. How local community knowledge about malaria affects insecticide-treated net use in northern Ghana. *Trop. Med. Int. Health* 10, 366–378.
- Albieri, A., Carrieri, M., Angelini, P., Baldacchini, F., Venturelli, C., Mascali Zeo, S., Bellini, R., 2010. Quantitative monitoring of *Aedes albopictus* in Emilia-Romagna, northern Italy: cluster investigation and geostatistical analysis. *Bull. Insectol.* 63, 209–216.
- Arensburger, P., Megy, K., Waterhouse, R.M., Abrudan, J., Amedeo, P., Antelo, B., Bartholomay, L., Bidwell, S., Caler, E., Camara, F., Campbell, C.L., Campbell, K.S., Casola, C., Castro, M.T., Chandramouliswaran, I., Chapman, S.B., Christley, S., Costas, J., Eisenstadt, E., Feschotte, C., Fraser-Liggett, C., Guigo, R., Haas, B., Hammond, M., Hansson, B.S., Hemingway, J., Hill, S.R., Howarth, C., Ignell, R., Kennedy, R.C., Kodira, C.D., Lobo, N.F., Mao, C., Mayhew, G., Michel, K., Mori, A., Liu, N., Naveira, H., Nene, V., Nguyen, N., Pearson, M.D., Pritham, E.J., Puiu, D., Qi, Y., Ranson, H., Ribeiro, J.M., Robertson, H.M., Severson, D.W., Shumway, M., Stanke, M., Strausberg, R.L., Sun, C., Sutton, G., Tu, Z.J., Tubio, J.M., Unger, M.F., Vandalingham, D.L., Vilella, A.J., White, O., White, J.R., Wondji, C.S., Wortman, J., Zdobnov, E.M., Birren, B., Christensen, B.M., Collins, F.H., Cornel, A., Dimopoulos, G., Hannick, L.I., Higgs, S., Lanzaro, G.C., Lawson, D., Lee, N.H., Muskavitch, M.A., Raikhel, A.S., Atkinson, P.W., 2010. Sequencing of *Culex quinquefasciatus* establishes a platform for mosquito comparative genomics. *Science* 330, 86–88.
- Assogba, B.S., Djogbénou, L., Saizonou, J., Diabaté, A., Dabiré, R.K., Gilles, J., Makoutodé, M., Baldet, T., 2014. Characterization of swarming and mating behaviour between *Anopheles coluzzii* and *Anopheles melas* in a sympatry area of Benin. *Acta Trop.* 132, S53–S63.
- Balestrino, F., Benedict, M.Q., Gilles, J.R., 2012. A new larval tray and rack system for improved mosquito mass rearing. *J. Med. Entomol.* 49, 595–605.
- Barat, L.M., Palmer, N., Basu, S., Worrall, E., Hanson, K., Mills, A., 2004. Do malaria control interventions reach the poor? A view through the equity lens. *Am. J. Trop. Med. Hyg.* 71, 174–178.
- Beier, J.C., Killeen, G.F., Githure, J., 1999. Short report: entomologic inoculation rates and *Plasmodium falciparum* malaria prevalence in Africa. *Am. J. Trop. Med. Hyg.* 61, 109–113.
- Beier, J.C., Keating, J., Githure, J.I., Macdonald, M.B., Impoinvil, D.E., Novak, R.J., 2008. Integrated vector management for malaria control. *Malar. J.* 7, S4.
- Bellini, R., Albieri, A., Balestrino, F., Carrieri, M., Porretta, D., Urbanelli, S., Calvitti, M., Moretti, R., Maini, S., 2010a. Dispersal and survival of *Aedes albopictus* (Diptera: Culicidae) males in Italian urban areas and significance for sterile insect technique application. *J. Med. Entomol.* 47, 1082–1091.
- Bellini, R., Albieri, A., Balestrino, F., Carrieri, M., Porretta, D., Urbanelli, S., Calvitti, M., Moretti, R., Maini, S., 2010b. Dispersal and survival of *Aedes albopictus* (Diptera: Culicidae) males in Italian urban areas and significance for sterile insect technique application. *J. Med. Entomol.* 47 (6), 1082–1091, <http://dx.doi.org/10.1603/ME09154>.
- Bellini, R., Medici, A., Puggioli, A., Balestrino, F., Carrieri, M., 2013a. Pilot field trials with *Aedes albopictus* irradiated sterile males in Italian urban areas. *J. Med. Entomol.* 50, 317–325.
- Bellini, R., Balestrino, F., Medici, A., Gentile, G., Veronesi, R., Carrieri, M., 2013b. Mating competitiveness of *Aedes albopictus* radio-sterilized males in large enclosures exposed to natural conditions. *J. Med. Entomol.* 50, 94–102.
- Bellini, R., Puggioli, A., Balestrino, F., Brunelli, P., Medici, A., Carrieri, M., 2014. Sugar administration to newly emerged *Aedes albopictus* males increases their survival probability and mating performance. *Acta Trop.* 132, S116–S123.
- Benedict, M.Q., Knols, B.G.J., Bossin, H.C., Howell, P.I., Mialhe, E., Caceres, C., Robinson, A.S., 2009. Colonisation and mass rearing: learning from others. *Malar. J.* 8, S4.
- Bernard, Q., 2012. Bases chimiques de la communication et des relations insectes-plantes chez deux espèces de moustiques. Master 2 «Sciences du vivant», Spécialité «Valorisation des Ressources Naturelles», Faculté des Sciences. Université de la Réunion, pp. 90.
- Bhatt, S., Gething, P.W., Brady, O.J., Messina, J.P., Farlow, A.W., Moyes, C.L., Drake, J.M., Brownstein, J.S., Hoen, A.G., Sankoh, O., Myers, M.F., George, D.B., Jaenisch, T., Wint, G.R., Simmons, C.P., Scott, T.W., Farrar, J.J., Hay, S.I., 2013. The global distribution and burden of dengue. *Nature* 496, 504–507.
- Bock, M.E., Reisen, W.K., Milby, M.M., 1983. Lifetime mating patterns of laboratory adapted *Culex tarsalis* males. *Mosq. News* 43, 350–354.
- Bohbot, J., Pitts, R.J., Kwon, H.W., Rützler, M., Robertson, H.M., Zwiebel, L.J., 2007. Molecular characterization of the *Aedes aegypti* odorant receptor gene family. *Insect Mol. Biol.* 16, 525–537.
- Bohbot, J.D., Dickens, J.C., 2009. Characterization of an enantioselective odorant receptor in the yellow fever mosquito *Aedes aegypti*. *PLoS One* 4, e7032.
- Bohbot, J.D., Dickens, J.C., 2010. Insect repellents: modulators of mosquito odorant receptor activity. *PLoS One* 5, e12138.
- Bohbot, J.D., Jones, P.L., Wang, G., Pitts, R.J., Pask, G.M., Zwiebel, L.J., 2011. Conservation of indole responsive odorant receptors in mosquitoes reveals an ancient olfactory trait. *Chem. Senses* 36, 149–160.
- Bourtzis, K., Dobson, S., Xi, Z., Rasgon, J., Calviti, M., Moreira, L.A., Bossin, H., Moretti, R., Baton, L.A., Hedges, G.L., Mavingui, P., Gilles, J.R.L., 2014. Harnessing mosquito–*Wolbachia* symbiosis for vector and disease control. *Acta Trop.* 132, S150–S163.
- Boyer, S., Toty, C., Jacquet, M., Lempérière, G., Fontenille, D., 2012. Evidence of multiple inseminations in the field in *Aedes albopictus*. *PLoS One* 7, e42040.
- Brown, J.E., McBride, C.S., Johnson, P., Ritchie, S., Paupy, C., Bossin, H.C., Lutomia, J., Fernandes-Salas, I., Ponlawat, A., Cornel, A.J., Black, I.V., Gorochotegui-Escalante, W.C., Urdenata-Marquez, N., Sylla, L., Slotman, M., Murray, M., Walker, K.O., Powell, C.J.R., 2011. Worldwide patterns of genetic differentiation imply multiple domestications of *Aedes aegypti*, a major vector of human diseases. *Proc. Biol. Sci.* 278, 2446–2454.
- Butail, S., Manoukis, N.C., Diallo, M., Ribeiro, J., Lehmann, T., Paley, D., 2012. Reconstructing the flight kinematics of swarming and mating behaviour in wild mosquitoes. *J. R. Soc. Interface* 7, 2624–2638.
- Butail, S., Manoukis, N.C., Diallo, M., Ribeiro, J.M., Paley, D.A., 2013. The dance of male *Anopheles gambiae* in wild mating swarms. *J. Med. Entomol.* 50, 552–559.
- Caldas de Castro, M., Yamagata, Y., Mtsiwa, D., Tanner, M., Utzinger, J., Keiser, J., Singer, B.H., 2004. Integrated urban malaria control: a case study in dar es salaam, Tanzania. *Am. J. Trop. Med. Hyg.* 71, 103–117.
- Calkins, C.O., Parker, A.G., 2005. Sterile insect quality. In: Dyck, V.A., Hendrichs, J., Robinson, A.S. (Eds.), *Sterile Insect Technique: Principles and Practice in Area-wide Integrated Pest Management*. Springer, Dordrecht, pp. 269–296.
- Carey, A.F., Wang, G., Su, C.Y., Zwiebel, L.J., Carlson, J.R., 2010. Odorant reception in the malaria mosquito *Anopheles gambiae*. *Nature* 464, 66–71.
- Carrieri, M., Albieri, A., Angelini, P., Baldacchini, F., Venturelli, C., Mascali Zeo, S., Bellini, R., 2011a. Surveillance of the chikungunya vector *Aedes albopictus* (Skuse) in Emilia-Romagna (northern Italy): organizational and technical aspects of a large scale monitoring system. *J. Vector Ecol.* 36, 108–116.
- Carrieri, M., Angelini, P., Venturelli, C., Maccagnani, B., Bellini, R., 2011b. *Aedes albopictus* (Diptera: Culicidae) population size survey in the 2007 Chikungunya outbreak area in Italy. I. Characterization of breeding sites and evaluation of sampling methodologies. *J. Med. Entomol.* 48, 1214–1225.
- Carrieri, M., Angelini, P., Venturelli, C., Maccagnani, B., Bellini, R., 2012. *Aedes albopictus* (Diptera: Culicidae) population size survey in the 2007 Chikungunya outbreak area in Italy. II: Estimating epidemic thresholds. *J. Med. Entomol.* 49, 388–399.
- Cator, L.J., Arthur, B.J., Harrington, L.C., Hoy, R.R., 2009. Harmonic convergence in the love songs of the dengue vector mosquito. *Science* 323, 1077–1079.
- Catteruccia, F., Crisanti, A., Wimmer, E.A., 2009. Transgenic technologies to induce sterility. *Malar. J.* 8, S7.
- Chadee, D.D., Gilles, J.R.L., 2014. The diel copulation periodicity of the mosquito, *Aedes aegypti* (L.) (Diptera: Culicidae) at indoor and outdoor sites in Trinidad, West Indies. *Acta Trop.* 132, S91–S95.
- Chambers, E.W., Hapairai, L., Peel, B.A., Bossin, H.C., Dobson, S.L., 2011. Male mating competitiveness of a *Wolbachia*-introgressed *Aedes polynesiensis* strain under semi-field conditions. *PLoS Negl. Trop. Dis.* 5, e1271.
- Chambers, E.W., Bossin, H.C., Ritchie, S.A., Russell, R.C., Dobson, S.L., 2013. Landing response of *Aedes (Stegomyia) polynesiensis* mosquitoes to coloured targets. *Med. Vet. Entomol.*, <http://dx.doi.org/10.1111/j.1365-2915.2012.01065.x>.
- Chanda, E., Masaninga, F., Coleman, M., Sikaala, C., Katebe, C., MacDonald, M., Baboo, K.S., Govere, J., Manga, L., 2008. Integrated vector management: the Zambian experience. *Malar. J.* 7, 19.
- Charlwood, J.D., 2011. Studies on the biology of male *Anopheles* Giles and *Anopheles funestus* Giles from southern Mozambique. *J. Vector Ecol.* 36, 382–394.
- Charlwood, J.D., Pinto, J., Sousa, C.A., Ferreira, C., do Rosario, V.E., 2002a. Male size does not affect mating success (of *Anopheles gambiae* from São Tomé). *Med. Vet. Entomol.* 16, 1–3.
- Charlwood, J.D., Pinto, J., Sousa, C.A., Madsen, H., Ferreira, C., do Rosario, V.E., 2002b. The swarming and mating behaviour of *Anopheles gambiae* s.s. (Diptera: Culicidae) from São Tomé Island. *J. Vector Ecol.* 27, 178–183.
- Charlwood, J.D., Thompson, R., Madsen, H., 2003. Observations on the swarming and mating behaviour of *Anopheles funestus* from southern Mozambique. *Malar. J.* 2, 2.

- Charlwood, J.D., Tomas, E.V., Salgueiro, P., Egyir-Yawson, A., Pitts, R.J., Pinto, J., 2011. Studies on the behaviour of peridomestic and endophagic M form *Anopheles gambiae* from a rice growing area of Ghana. *Bull. Entomol. Res.* 101, 533–539.
- Charlwood, J.D., Tomas, E.V., Salgueiro, P., Egyir-Yawson, A., Pitts, R.J., Pinto, J., 2012. Feeding frequency and survival of *Anopheles gambiae* in a rice-growing area in Ghana. *Med. Vet. Entomol.* 26, 263–270.
- Clements, A.N., 1999. *The Biology of Mosquitoes*, 2. CABI Publishing Oxon, UK.
- Coetzee, M., Craig, M., le Sueur, D., 2000. Distribution of African malaria mosquitoes belonging to the *Anopheles gambiae* complex. *Parasitol. Today* 16, 74–77.
- Coetzee, Koekemoer, 2013. Molecular systematics and insecticide resistance in the major African Malaria vector *Anopheles funestus*. *Annu. Rev. Entomol.* 58, 393–412.
- Coetzee, M., Hunt, R.H., Wilkerson, R., Torre, A.D., Coulbaly, M.B., Besansky, N.J., 2013. *Anopheles coluzzii* and *Anopheles amharicus*, new members of the *Anopheles gambiae* complex. *Zootaxa* 3619, 246–274.
- Craig, M.H., Snow, R.W., le Sueur, D., 1999. A climate-based distribution model of malaria transmission in sub-Saharan Africa. *Parasitol. Today* 15, 105–111.
- Dabiré, K., Sawadogo, P., Diabaté, A., Toé, H., Kengne, P., Ouari, A., Costantini, C., Gouagna, C., Simard, F., Baldet, T., Lehmann, T., Gibson, G., 2013. Assortative mating in mixed swarms of the mosquito *Anopheles gambiae* s.s. M and S molecular forms, in Burkina Faso, West Africa. *Med. Vet. Entomol.*, <http://dx.doi.org/10.1111/j.1365-2915.2012.01049.x>.
- Dabiré, K.R., Sawadogo, P.S., Hien, D.F., Maïga, H., Millogo, A., Baldet, T., Simard, F., Gouagna, L.-C., Diabaté, A., Gibson, G., Lees, R.S., Gilles, J.R.L., 2014. Occurrence of natural *Anopheles arabiensis* swarms in an urban area of Bobo-Dioulasso city, Burkina Faso, West Africa. *Acta Trop.* 132, S35–S41.
- Dahan, Y.L., Koekemoer, L.L., 2014. Analysis of the genitalia rotation in the male *Anopheles funestus* (Diptera: Culicidae). *Acta Trop.* 132, S20–S25.
- Damiens, D., Benedict, M.Q., Wille, M., Gilles, J.R., 2012. An inexpensive and effective larval diet for *Anopheles arabiensis* (Diptera: Culicidae): eat like a horse, a bird, or a fish? *J. Med. Entomol.* 49, 1001–1011.
- Damiens, D., Vreysen, M.J.B., Gilles, J.R.L., 2013. *Anopheles arabiensis* sperm production after genetic manipulation dieltrin treatment, and irradiation. *J. Med. Entomol.* 50, 314–316.
- Dao, A., Adamou, A., Yaro, A.S., Maïga, H.M., Kassogue, Y., Traoré, S.F., Lehmann, T., 2008. Assessment of alternative mating strategies in *Anopheles gambiae*: does mating occur indoors? *J. Med. Entomol.* 45, 643–652.
- de Meillon, B., Sebastian, A., Khan, Z.H., 1967. Cane-sugar feeding in *Culex pipiens fatigans*. *Bull. World Health Organ.* 36, 53–65.
- de Oliveira Carvalho, D., Costa-da-Silva, A.L., Lees, R.S., Capurro, M.L., 2014. Two step male release strategy using transgenic mosquito lines to control transmission of vector-borne diseases. *Acta Trop.* 132, S170–S177.
- Djogbénu, L., Pasteur, N., Bio-Bangana, S., Baldet, T., Irish, S., Akogbété, M., Weill, M., Chandre, F., 2010. Malaria vectors in the Republic of Benin: distribution of species and molecular forms of the *Anopheles gambiae* complex. *Acta Trop.* 114, 116–122.
- Downes, J.A., 1969. The swarming and mating flight of Diptera. *Annu. Rev. Entomol.* 14, 271–298.
- Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215–223.
- Eriksoon, M., 2012. Chemical investigations of species in the genus *Hoya* (Apocynaceae). In: Masters Thesis. Royal Institute of Technology, Stockholm, Sweden.
- Ferguson, F.M., John, B., Ng'habi, K., Knols, B.G.J., 2005. Redressing the sex imbalance in knowledge of vector biology. *Trends Evol. Ecol.* 20, 202–209.
- Ferveur, J.F., 2005. Cuticular hydrocarbons: their evolution and roles in *Drosophila* pheromonal communication. *Behav. Genet.* 35, 279–295.
- Foster, W.A., 1995. Mosquito sugar feeding and reproductive energetics. *Annu. Rev. Entomol.* 40, 443–474.
- Fu, G., Lees, R.S., Nimmo, D., Aw, D., Jin, L., Gray, P., Berendonk, T.U., White-Cooper, H., Scaife, S., Kim Phuc, H., Marinotti, O., Jasinskiene, N., James, A.A., Alphey, L., 2010. Female-specific flightless phenotype for mosquito control. *PNAS* 107, 4550–4554.
- Gary, R.E., Foster, W.A., 2004. *Anopheles gambiae* feeding and survival on honeydew and extra-floral nectar of peridomestic plants. *Med. Vet. Entomol.* 18, 102–107.
- Gary, R.E., Cannon, J.W., Foster, W.A., 2009. Effect of sugar on male *Anopheles gambiae* mating performance, as modified by temperature, space, and body size. *Parasites Vectors* 2, 19.
- Gato, R., Companioni, A., Bruzon, R.Y., Menendez, Z., González, A., Rodríguez, M., 2014. Release of thiotepa sterilized males on cages populations of *Aedes aegypti*: life table analysis. *Acta Trop.* 132, S164–S169.
- Gato, R., Lees, R.S., Bruzon, R.Y., Companioni, A., Menendez, Z., González, A., Rodríguez, M., 2013. Indoor large cages study of suppression of *Aedes aegypti* by release of thiotepa sterilized mosquitoes. *Acta Trop.* (submitted to Memórias do Instituto Oswaldo Cruz on 30 October 2013).
- Gilles, J.R.L., Schetelig, M., Scolari, F., Marec, F., Capurro, M., Franz, G., Bourtzis, K., 2014. Towards mosquito SIT programmes: exploring genetic, molecular, mechanical and behavioural methods of sex separation in mosquitoes. *Acta Trop.* 132, S178–S187.
- Gouagna, L.C., Kerampran, R., Lebon, C., Bregngues, C., Toty, C., Fontenille, D., 2014. Sugar-source preference, sugar intake and relative nutritional benefits in *Anopheles arabiensis* males. *Acta Trop.* 132, S70–S79.
- Gouagna, L.C., Poueme, R.S., Dabiré, K.R., Ouedraogo, J.B., Fontenille, D., Simard, F., 2010. Patterns of sugar feeding and host plant preferences in adult males of *An. gambiae* (Diptera: Culicidae). *J. Vector Ecol.* 35, 267–276.
- Gubler, D., 2004. The changing epidemiology of yellow fever and dengue, 1900 to 2003: full circle? *Comp. Immunol. Microbiol. Inf. Dis.* 27, 319–330.
- Guillaumot, L., Ofanoa, R., Swillen, L., Singh, N., Bossin, H.C., Schaffner, F., 2012. Distribution of *Aedes albopictus* (Diptera: Culicidae) in southwestern Pacific countries, with a first report from the Kingdom of Tonga. *Parasites Vectors* 5, 247.
- Guinovart, C., Navia, M.M., Tanner, M., Alonso, P.L., 2006. Malaria: burden of disease. *Curr. Mol. Med.* 6, 137–140.
- Halle, E.A., Nicole Fox, A., Zwiebel, L.J., Carlson, J.R., 2004. Olfaction: mosquito receptor for human-sweat odorant. *Nature* 427, 212–213.
- Hapairai, L.K., Cheong-Sang, M.A., Sinkins, S.P., Bossin, H.C., 2013a. Population studies of the filarial vector *Aedes polynesiensis* (Diptera: Culicidae) in two island settings of French Polynesia. *J. Med. Entomol.* 50, 965–976 [submitted].
- Hapairai, L.K., Joseph, H., Cheong-Sang, M.A., Melrose, W., Ritchie, A.S., Burkot, T.R., Sinkins, S.P., Bossin, H.C., 2013b. Field evaluation of selected traps and lures for monitoring the filarial and arbovirus vector, *Aedes polynesiensis* (Diptera: Culicidae), in French Polynesia. *J. Med. Entomol.* 50, 731–739 [submitted].
- Hapairai, L.K., Marie, J., Sinkins, S.P., Bossin, H.C., 2014. Effect of temperature and larval density on *Aedes polynesiensis* (Diptera: Culicidae) laboratory rearing productivity and potential male performance. *Acta Trop.* 132, S108–S115.
- Hassan, M., El-Motasim, W., Ahmed, R., El-Sayed, B., 2010. Prolonged colonisation, irradiation, and transportation do not impede mating vigour and competitiveness of male *Anopheles arabiensis* mosquitoes under semi-field conditions in Northern Sudan. *Malar. J.* 1, 2.
- Hassan, M.M., Zain, H.M., Basheer, M.A., Elhaj, H.F., El-Sayed, B.B., 2014. Swarming and mating behaviour of male *Anopheles arabiensis* Patton (Diptera: Culicidae) in an area of sterile insect techniques project in Dongola, northern Sudan. *Acta Trop.* 132, S64–S69.
- Hay, S.I., Rogers, D.J., Toomer, J.F., Snow, R.W., 2000. Annual *Plasmodium falciparum* entomological inoculation rates across Africa: literature survey, internet access and review. *Trans. R. Soc. Trop. Med. Hyg.* 94, 113–127.
- Hemingway, J., 2004. Taking aim at mosquitoes. *Nature* 430, 936.
- Hendrichs, J., Ortis, G., Liedo, P., Schwarz, A., 1983. Six years of successful medfly programme in Mexico and Guatemala. In: Cavalloro, R. (Ed.), *Fruit flies of economic importance. Proceedings of a CEC/IOBC International Symposium*, 16–19 November 1982, Athens, pp. 353–365.
- Hill, C.A., Fox, A.N., Pitts, R.J., Kent, L.B., Tan, P.L., Chrystal, M.A., Cravchik, A., Collins, F.H., Robertson, H.M., Zwiebel, L.J., 2002. G protein-coupled receptors in *Anopheles gambiae*. *Science* 298, 176–178.
- Holt, R.A., Subramanian, G.M., Halpern, A., Sutton, G.G., Charlab, R., Nusskern, D.R., Winkler, P., Clark, A.G., Ribeiro, J.M., Wides, R., Salzberg, S.L., Loftus, B., Yandell, M., Majoros, W.H., Rusch, D.B., Lai, Z., Kraft, C.L., Abril, J.F., Anthouard, V., Arensburg, P., Atkinson, P.W., Baden, H., de Berardinis, V., Baldwin, D., Benes, V., Biedler, J., Blass, C., Bolanos, R., Boscus, D., Barnstead, M., Cai, S., Center, A., Chaturvedi, K., Christophides, G.K., Chrystal, M.A., Clamp, M., Cravchik, A., Curwen, V., Dana, A., Delcher, A., Dew, I., Evans, C.A., Flanigan, M., Grundschober-Freimoser, A., Friedli, L., Gu, Z., Guan, P., Guigo, R., Hillenmeyer, M.E., Hladun, S.L., Hogan, J.R., Hong, Y.S., Hoover, J., Jaillon, O., Ke, Z., Kodira, C., Kokoza, E., Koutsos, A., Letunic, I., Levitsky, A., Liang, Y., Lin, J.J., Lobo, N.F., Lopez, J.R., Malek, J.A., McClintock, T.C., Meister, S., Miller, J., Mobarry, J., Mongin, E., Murphy, S.D., O'Brochta, D.A., Pfannkoch, C., Qi, R., Regier, M.A., Remington, K., Shao, H., Sharakhova, M.V., Sitter, C.D., Shetty, J., Smith, T.J., Strong, R., Sun, J., Thomasova, D., Ton, L.Q., Topalis, P., Tu, Z., Unger, M.F., Walenz, B., Wang, A., Wang, J., Wang, M., Wang, X., Woodford, K.J., Wortman, J.R., Wu, M., Yao, A., Zdobnov, E.M., Zhang, H., Zhao, Q., Zhao, S., Zhu, S.C., Zhimulev, I., Coluzzi, M., della Torre, A., Roth, C.W., Louis, C., Kalush, F., Mural, R.J., Myers, E.W., Adams, M.D., Smith, H.O., Broder, S., Gardner, M.J., Fraser, C.M., Birney, E., Bork, P., Brey, P.T., Venter, J.C., Weissenbach, J., Kafatos, F.C., Collins, F.H., Hoffman, S.L., 2002. The genome sequence of the malaria mosquito *Anopheles gambiae*. *Science* 298, 129–149.
- Howell, P.I., Knols, B.G., 2009. Male mating biology. *Malar. J.* 8, S8.
- Hughes, D.T., Pelletier, J., Luetje, C.W., Leal, W.S., 2010. Odorant receptor from the southern house mosquito narrowly tuned to the oviposition attractant skatole. *J. Chem. Ecol.* 36, 797–800.
- Iatrou, K., Biessmann, H., 2008. Sex-biased expression of odorant receptors in antennae and palps of the African malaria vector *Anopheles gambiae*. *Insect Biochem. Mol. Biol.* 38, 268–274.
- Iyaloo, D.P., Elahee, K.B., Bheecarry, A., Lees, R.S., 2014. Guidelines to site selection for population surveillance and mosquito control trials: a case study from Mauritius. *Acta Trop.* 132, S140–S149.
- Imponvil, D.E., Kongere, J.O., Foster, W.A., Njiru, B.N., Killeen, G.F., Githure, J.I., Beier, J.C., Hassanali, A., Knols, B.G.J., 2004. Feeding and survival of the malaria mosquito *Anopheles gambiae* on plants growing in Kenya. *Med. Vet. Entomol.* 18, 108–115.
- Kennedy, J.S., 1975. Insect dispersal. In: Pimentel, D. (Ed.), *Insects Science & Society*. New York Academic Press, New York, pp. 103–119.
- Kerampran, R., 2012. Etude des relations entre acquisition des ressources et fitness chez les mâles d'*Anopheles arabiensis* (Diptères: Culicidae): Approches comportementale, physiologique et biochimique. Master 2 Biodiversité et Ecosystèmes Tropicaux (BEST), Spécialité « Biodiversité et Ecosystèmes Naturels ». Faculté des Sciences, Université de la Réunion, pp. 50.
- Kittayapong, P., Yoksan, S., Chansang, U., Chansang, C., Bhumiratana, A., 2008. Suppression of dengue transmission by application of integrated vector control strategies at sero-positive GIS-based Foci. *Am. J. Trop. Med. Hyg.* 78, 70–76.
- Korenromp, E.L., Williams, B.G., Gouws, E., Dye, C., Snow, R.W., 2003. Measurement of trends in childhood malaria mortality in Africa: an assessment of progress towards targets based on verbal autopsy. *Lancet Inf. Dis.* 3, 349–358.

- Koul, O., Cuperus, G.W., Elliot, N. (Eds.), 2008. *Areawide Pest Management: Theory and Implementation*. CAB International, Wallingford.
- Labbé, G.M., Scaife, S., Morgan, S.A., Curtis, Z.H., Alphey, L., 2012. Female-specific flightless (fsRIDL) phenotype for control of *Aedes albopictus*. *PLoS Negl. Trop. Dis.* 6, e1724.
- Lepage, D., Bordenstein, S.R., 2013. Wolbachia: can we save lives with a great pandemic? *Trends Parasitol.*, 003, <http://dx.doi.org/10.1016/j.pt.2013.06>.
- Liroff, R., 2000. Doctoring malaria badly: the global campaign to ban DDT. *Br. Med. J.* 321, 1404–1405.
- Lounibos, L.P., Lima, D.C., Lourenco de Oliveira, R., 1998. Prompt mating of released *Anopheles darlingi* in western Amazonian Brazil. *J. Am. Mosq. Control Assoc.* 14, 210–213.
- Madakacherry, M., Lees, R.S., Gilles, J., 2014. *Aedes albopictus* (Skuse) males in laboratory and semi-field cages: Release ratios and mating competitiveness. *Acta Trop.* 132, S124–S129.
- Maïga, H., 2011. Analyse des ressources énergétiques nécessaires aux activités d'essaimage et d'accouplement chez *Anopheles gambiae*. In: Master International d'Entomologie médicale et Vétérinaire (MIE) UAC/UM2/CREC/IRSP/IRD, Cotonou, Bénin., pp. 25.
- Maïga, H., Dabiré, K., Lehmann, T., Tripet, F., Diabaté, A., 2012. Variation in energy reserves and role of body size in the mating system of *Anopheles gambiae*. *J. Vector Ecol.* 37, 289–297.
- Maïga, H., Niang, A., Sawadogo, S., Dabiré, R., Lees, R.S., Gilles, J.R.L., Tripet, F., Diabaté, A., 2014. Role of nutritional reserves and body size in *Anopheles gambiae* males mating success. *Acta Trop.* 132, S102–S107.
- Manoukis, N.C., Diabaté, A., Abdoulaye, A., Diallo, M., Dao, A., Yaro, A., Robeiro, J., Lehmann, T., 2009. Structure and dynamics of male swarms of *Anopheles gambiae*. *J. Med. Entomol.* 46, 227–235.
- Manoukis, N.C., Butail, S., Shishika, D.L., Paley, D.A., Ribeiro, J.M.C., 2014. Stereoscopic video analysis of *Anopheles gambiae* behavior in the field: challenges and opportunities. 3D video analysis of male *Anopheles gambiae* mating behavior in the field: challenges and opportunities. *Acta Trop.* 132, S80–S85.
- Marie, J., Bossin, H.C., 2013. First Record of *Wyeomyia* (*Wyeomyia*) *mitchellii* (Diptera: Culicidae) in French Polynesia. *J. Med. Entomol.* 50, 37–42.
- Martin, S., Drijfhout, F., 2013. A review of ant cuticular hydrocarbons. *J. Chem. Ecol.* 35, 1151–1161.
- Matthews, G.A., Dobson, H.M., Nkot, P.B., Wiles, T.L., Birchmore, M., 2009. Preliminary examination of integrated vector management in a tropical rainforest area of Cameroon. *Trans. R. Soc. Trop. Med. Hyg.* 103, 1098–1104.
- Medici, A., Carrieri, M., Scholte, E.-J., MacCagnani, B., Dindo, M.L., Bellini, R., 2011. Studies on *Aedes albopictus* larval mass-rearing optimization. *J. Econ. Entomol.* 104, 266–273.
- Mercer, D.R., Marie, J., Bossin, H.C., Faaruia, M., Tetuanui, A., Cheong-Sang, M.A., Dobson, S.L., 2012a. Estimation of population size and dispersal of *Aedes polynesiensis* on Toamaro motu, French Polynesia. *J. Med. Entomol.* 49, 971–980.
- Mercer, D.R., Bossin, H.C., Cheong-Sang, M.A., O'Connor, L., Dobson, S.L., 2012b. Monitoring temporal abundance and spatial distribution of *Aedes polynesiensis* using BG-Sentinel® traps in neighboring habitats on Raiatea, Society Archipelago, French Polynesia. *J. Med. Entomol.* 49 (1), 51–60.
- Molineaux, L., Gramiccia, G., 1980. The Garki Project. World Health Organisation, Geneva.
- Müller, G.C., Xue, R.D., Schlein, Y., 2010. Seed pods of the carob tree *Ceratonia siliqua* are a favored sugar source for the mosquito *Aedes albopictus* in coastal Israel. *Acta Trop.* 116, 235–239.
- Müller, G.C., Xue, R.D., Schlein, Y., 2011. Differential attraction of *Aedes albopictus* in the field to flowers, fruits and honeydew. *Acta Trop.* 118, 45–49.
- Munhenga, G., Basil, D., Brooke, T., Chirwa, F., Hunt, R., Govender, D., Coetzee, M., Koenkemoer, L., 2011. Evaluating the potential of the sterile insect technique for malaria control: Relative fitness and mating compatibility between laboratory colonized and a wild population of *Anopheles arabiensis* from the Kruger National Park, South Africa. *Parasites Vectors* 4, 208.
- Najera, J.A., 2001. Malaria control: achievements, problems and strategies. *Parasitologia* 11, 391–406.
- Nam, V.S., Nguyen, T.Y., Tran, V.P., Truong, U.N., Le, Q.M., Le, V.L., Le, T.N., Bektas, A., Briscoe, A., Aaskov, J.G., Ryan, P.A., Kay, B.H., 2005. Elimination of dengue by community programs using *Mesocyclops* (Copepoda) against *Aedes aegypti* in central Vietnam. *Am. J. Trop. Med. Hyg.* 72, 67–73.
- Nene, V., Wortman, J.R., Lawson, D., Haas, B., Kodira, C., Tu, Z.J., Loftus, B., Xi, Z., Megy, K., Grabherr, M., Ren, Q., Zdobnov, E.M., Lobo, N.F., Campbell, K.S., Brown, S.E., Bonaldo, M.F., Zhu, J., Sinkins, S.P., Hogenkamp, D.G., Amedeo, P., Arensburg, P., Atkinson, P.W., Bidwell, S., Biedler, J., Birney, E., Bruggner, R.V., Costa, J., Coy, M.R., Crabtree, J., Crawford, M., DeBruyn, B., Decaprio, D., Eigelmeier, K., Eisenstadt, E., El-Dorri, H., Gelbart, W.M., Gomes, S.L., Hammond, M., Hannick, L.L., Hogan, J.R., Holmes, M.H., Jaffe, D., Johnston, J.S., Kennedy, R.C., Koo, H., Kravitz, S., Kriventseva, E.V., Kulp, D., Labutti, K., Lee, E., Li, S., Lovin, D.D., Mao, C., Maucei, E., Menck, C.F., Miller, J.R., Montgomery, P., Mori, A., Nascimento, A.L., Naveira, H.F., Nusbbaum, C., O'leary, S., Orvis, J., Perlea, M., Quesneville, H., Reidenbach, K.R., Rogers, Y.H., Roth, C.W., Schneider, J.R., Schatz, M., Shumway, M., Stanke, M., Stinson, E.O., Tubio, J.M., Vanzee, J.P., Verjovski-Almeida, S., Werner, D., White, O., Wyder, S., Zeng, Q., Zhao, Q., Zhao, Y., Hill, C.A., Raikhel, A.S., Soares, M.B., Knudson, D.L., Lee, N.H., Galagan, J., Salzberg, S.L., Paulsen, I.T., Dimopoulos, G., Collins, F.H., Birren, B., Fraser-Liggett, C.M., Severson, D.W., 2007. Genome sequence of *Aedes aegypti*, a major arbovirus vector. *Science* 316, 1718–1723.
- Nijhout, H.F., Craig Jr., G.B., 1971. Reproductive isolation in *Stegomyia* mosquitoes. III. Evidence for a sexual pheromone. *Entomol. Exp. Appl.* 14, 399–412.
- Noor, A.M., Amin, A.A., Akhwale, W.S., Snow, R.W., 2007. Increasing coverage and decreasing inequity in insecticide-treated bed net use among rural Kenyan children. *PLoS Med.* 4, e255.
- OAU/BAR, 2000. PATTEC—Pan African Tsetse and Trypanosomiasis Eradication Campaign. Available from: <http://www.oau-ibar.org/lome2000> Accessed 10 June 2013.
- O'Connor, L., Plichart, C., Sang, A.C., Brelsfoard, C.L., Bossin, H.C., Dobson, S.L., 2012. Open release of male mosquitoes infected with a *Wolbachia biopesticide*: field performance and infection containment. *PLoS Negl. Trop. Dis.* 6, e4797.
- Oliva, C.F., Damiens, D., Benedict, M.Q., 2014a. Male reproductive biology of *Aedes* mosquitoes. *Acta Trop.* 132, S12–S19.
- Oliva, C.F., Vreysen, M.J.B., Dupé, S., Gilles, J.R.L., Gouagna, L.-C., Lees, R.S., Chhem, R., 2014b. Current status and future challenges for controlling malaria with the sterile insect technique: technical and social perspectives. *Acta Trop.* 132, S130–S139.
- Oliva, C.F., Jacquet, M., Gilles, J., Lemperiere, G., Maquart, P.-O., Quilici, S., Schooneman, F., Vreysen, M.J.B., Boyer, S., 2012. The sterile insect technique for controlling populations of *Aedes albopictus* (Diptera: Culicidae) on reunion island: mating vigour of sterilized males. *PLoS One* 7, e49414.
- Ouedraogo, R., 2008. Mise en évidence de l'alimentation sucrée chez les vecteurs du paludisme dans deux localités de l'Ouest du Burkina Faso. In: Diplôme d'Etude Approfondie (DEA). Faculty of Science, Université Polytechnique Bobo Dioulasso, pp. 47.
- PAAT, 2000. Programme Against African Trypanosomiasis. In: Newsletter No. 8, December 2000.
- Papathanas, P.A., Bossin, H.C., Benedict, M.Q., Catteruccia, F., Malcolm, C.A., Alphey, L., Crisanti, A., 2009. Sex separation strategies: past experience and new approaches. *Malar. J.* 8, S5.
- Pelletier, J., Hughes, D.T., Luetje, C.W., Leal, W.S., 2010. An odorant receptor from the southern house mosquito *Culex pipiens quinquefasciatus* sensitive to oviposition attractants. *PLoS One* 5, e10090.
- Pennetier, C., Warren, B., Dabiré, K., Russell, I., Gibson, G., 2010. Singing on the wing as a mechanism for species recognition in the malarial mosquito *Anopheles gambiae*. *Curr. Biol.* 20, 131–136.
- Phuc, H.K., Andreasen, M.H., Burton, R.S., Vass, C., Epton, M.J., Pape, G., Fu, G., Condon, K.C., Scaife, S., Donnelly, C.A., Coleman, P.G., White-Cooper, H., Alphey, L., 2007. Late-acting dominant lethal genetic systems and mosquito control. *BMC Biol.* 5, 11.
- Pitts, R.R., Mozuraitis, R., Gauvin-Bialecki, A., Lemperiere, G., 2014. The roles of kairomones, synomones and pheromones in the chemically-mediated behaviour of male mosquitoes. *Acta Trop.* 132, S26–S34.
- Polerstock, A.R., Eigenbrode, S.D., Klodwen, M.J., 2002. Mating alters the cuticular hydrocarbons of female *Anopheles gambiae* sensu stricto and *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 39, 545–552.
- Poueme, R., 2008. Etude du comportement trophique des mâles d'*Anopheles* en rapport avec le sucre des plantes. In: Master International d'Entomologie médicale et Vétérinaire (MIE) UAC/UM2/CREC/IRSP/IRD. Cotonou, Bénin, pp. 20.
- Puggioli, A., Balestrino, F., Soliban, S.M., Madakacherry, O., Dindo, M.L., Bellini, R., Gilles, J.R.L., 2013. Efficiency of three diets for larval development in mass rearing *Aedes albopictus* (Diptera: Culicidae). *J. Med. Entomol.* 50, 819–825.
- Reisen, W.K., Sakai, R.K., Baker, R.H., Azra, K., Niaz, S., 1982. *Anopheles culicifacies*: observations on population ecology and reproductive behavior. *Mosq. News* 42, 93–101.
- Roberts, D.R., Andre, R.G., 1994. Insecticide resistance issues in vector-borne disease control. *Am. J. Trop. Med. Hyg.* 50, 21–34.
- Robinson, A.S., Knols, B.G.J., Voigt, G., Hendrichs, J., 2009. Conceptual framework and rationale. *Malar. J.* 8, S1.
- Rudolfs, W., 1922. Chemotropism of mosquitoes. *Bull. N. J. Agric. Exp. Stn. No.*, 367.
- Sachs, J., Malaney, P., 2002. The economic and social burden of malaria. *Nature* 415, 680–685.
- Sawadogo, P., Diabaté, A., Sanon, A., Toé, H., Baldet, T., Gibson, G., Gilles, J., Simard, F., Sinkins, S., Dabiré, K., 2013a. Effects of age and size on *Anopheles gambiae* s.s. male mosquito mating success. *J. Med. Entomol.* 50, 285–293.
- Sawadogo, P., Costantini, C., Pennetier, C., Diabaté, A., Gibson, G., Dabiré, K., 2013b. Influence of circadian rhythms and environmental factors on the timing of natural swarming behavior in *Anopheles gambiae* M and S molecular forms in Burkina Faso, West Africa. *Parasites Vectors*, in press.
- Sawadogo, P.S., Diabaté, A., Gnankinié, O., Toé, K.H., Rouamba, J., Ouari, A., Baldet, T., Simard, F., Costantini, C., Lees, R.S., Gilles, J., Gibson, G., Dabiré, K.R., 2014. Swarming behaviour in natural populations of *Anopheles gambiae* and *An. coluzzii*: Review of 4 years survey in rural areas of sympatry, Burkina Faso (West Africa). *Acta Trop.* 132, S42–S52.
- Service, M.W., 1997. Mosquito (Diptera: Culicidae) dispersal—the long and short of it. *J. Med. Entomol.* 34, 579–588.
- Shiff, C., 2002. Integrated approach to malaria control. *Clin. Microbiol. Rev.* 15, 278–298.
- Slooten, E., Lambert, D.M., 1984. Evolutionary studies of the New Zealand coastal mosquito *Opifex fuscus* (Hutton) II. Competition for mates. *Behaviour* 85, 1–12.
- Smith, S.M., Gadawski, R.M., 1994. Nectar feeding by the early-spring mosquito *Aedes provocans*. *Med. Vet. Entomol.* 8, 201–213.
- Stone, C.M., Taylor, R.M., Roitberg, B.D., Foster, W.A., 2009. Sugar deprivation reduces insemination of *Anopheles gambiae* (Diptera: Culicidae), despite daily recruitment of adults, and predicts decline in model populations. *J. Med. Entomol.* 46, 1327–1337.
- Sullivan, R.T., 1981. Insect swarming and mating. *Florida Entomol.* 64, 44–65.

- Takken, W., Charlwood, J.D., Billingsley, P.F., Gort, G., 1998. Dispersal and survival of *Anopheles funestus* and *A. gambiae* s.l. (Diptera: Culicidae) during the rainy season in southeast Tanzania. *Bull. Entomol. Res.* 88, 561–566.
- Tapia-Conyer, R., Betancourt-Cravioto, M., Méndez-Galván, J., 2012. Dengue: an escalating public health problem in Latin America. *Paediatr. Int. Child Health* 32, 14–17.
- Therawiwat, M., Fungladda, W., Kaewkungwal, J., Imamee, N., Steckler, A., 2005. Community-based approach for prevention and control of dengue haemorrhagic fever in Kanchanaburi province, Thailand. *Southeast Asian J. Trop. Med. Public Health* 36, 1439–1449.
- Townson, H., Nathan, M.B., Zaim, M., Guillet, P., Manga, L., Bos, R., Kindhauser, M., 2005. Exploiting the potential of vector control for disease prevention. *Bull. World Health Organ.* 83, 942–947.
- Turusov, V., Rakitsky, V., Tomatis, L., 2002. Dichlorodiphenyltrichloroethane (DDT): ubiquity, persistence, and risks. *Environ. Health Perspect.* 110, 125–128.
- van den Berg, H., von Hildebrand, A., Ragunathan, V., Das, P.K., 2007. Reducing vector-borne disease by empowering farmers in integrated vector management. *Bull. World Health Organ.* 85, 561–566.
- Vreysen, M.J.B., Robinson, A.S., Hendrichs, J. (Eds.), 2007. *Area-wide Control of Insect Pests. From Research to Field Implementation*, Dordrecht, The Netherlands. Springer.
- Wang, G., Carey, A.F., Carlson, J.R., Zwiebel, L.J., 2010. Molecular basis of odor coding in the malaria vector mosquito *Anopheles gambiae*. *PNAS* 107, 4418–4423.
- World Health Organisation, 2008. *WHO position statement on integrated vector management*. *Weekly Epidemiol. Rec.* 83, 177–181.
- World Health Organisation, 2012. *World Malaria Report 2012*. World Health Organisation, Geneva.
- Wyss, J.H., 2000. Screwworm eradication in the Americas. *Ann. N.Y. Acad. Sci.* 916, 186–193.
- Yahouédo, G.A., Djogbénu, L., Saïzonou, J., Assogba, B.S., Gilles, J., Maïga, H., Diabaté, A., Mouline, K., Soukou, B.K., Simard, F., 2014. Effect of three larval diets on larval development and male sexual performance of *Anopheles gambiae* s.s. *Acta Trop.* 132, S96–S101.
- Yamada, H., Soliban, S.M., Vreysen, M.J.B., Chadee, D.D., Gilles, J.R.L., 2013. Eliminating female *Anopheles arabiensis* by spiking blood meals with toxicants as a sex separation method in the context of the sterile insect technique. *Parasites Vectors* 6, 197.
- Yuval, B., 1992. The other habit—sugar feeding by mosquitoes. *Bull. Soc. Vector Ecol.* 17, 150–156.
- Yuval, B., Wekesa, J.W., Washino, R.K., 1993. Effects of body size on swarming behavior and mating success of male *Anopheles freeborni* (Diptera: Culicidae). *J. Insect Behav.* 6, 333–342.
- Yuval, B., Holliday-Hanson, M., Washino, R.K., 1994. Energy budget of swarming male mosquitoes. *Ecol. Entomol.* 19, 74–78.
- Zaim, M., Guillet, P., 2002. Alternative insecticides: an urgent need. *Trends Parasitol.* 18, 161–163.