Chapter 8
Feeding and Mating Behaviour of African Fruit Flies

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Abstract The majority of African fruit fly species are controlled using behavioural methods (e.g. attract and kill). Sterile Insect Technique (SIT) has also been successfully used for a few African fruit fly pests, mostly outside of the African region. A thorough understanding of the feeding and mating behaviour of fruit fly pests is required when using behavioural control methods and SIT for fruit fly control. The feeding and mating behaviour of key African fruit fly pests are reviewed. Feeding and mating behaviours have been elucidated for only a few species with a wider global distribution. For the remaining *Ceratitis*, *Bactrocera* and *Dacus* species with a limited worldwide distribution, there are still important knowledge gaps in their behavioural ecology. With horticulture expanding in Africa and increasing trade of horticultural produce from the region, it is important that these knowledge gaps are filled so that control methods can be optimised.

Keywords Behaviour • *Ceratitis* • *Bactrocera* • *Dacus* • *Zeugodacus* • Africa

1 Introduction

African fruit fly pests are mainly monitored and controlled using attractive food baits and male lures (Ekesi et al. 2007; Manrakhan 2006). For control, food baits and male lures are combined with a toxin or pathogen in an attract and annihilate approach; adult fruit flies are attracted to the bait/ lure and killed by the toxin or pathogen (Cunningham 1989; Roessler 1989). Such behavioural control methods are effective and limit insecticide use, but their efficacy can be influenced by a number of intrinsic (e.g genetic and physiological factors) and extrinsic (e.g climate, host abundance) factors (Foster and Harris 1997). As such, a thorough understanding of the feeding and mating behaviour of each pest species is essential for the optimisation of control methods.

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For some fruit fly pests, the Sterile Insect Technique (SIT) has also been successfully used worldwide as a method for prevention, containment, suppression and eradication (Enkerlin 2005). To date the use of SIT in Africa is still limited. Effectiveness of SIT programmes are dependent on successful mating of sterile males with wild-type females and the subsequent induction of reproductive failure (Perez-Staples et al. 2012). Given that most tropical and subtropical fruit flies have complex mating systems (Burk 1981), a detailed understanding of each mating system is crucial for successful development and optimisation of SIT (Hendrichs et al. 2002).

Here I review the current status of knowledge on the feeding and mating behaviour of key fruit fly pest species in Africa grouped under four genera: *Ceratitis*, *Bactrocera, Zeugodacus* and *Dacus*. Future research needs required to fill the gaps in our understanding of feeding and mating behaviour of these African fruit fly pests are also discussed.

2 Feeding Behaviour of African Fruit Flies

Fruit flies only feed during the larval and adult stages (Christenson and Foote 1960). Frugivorous fruit fly larvae feed on the fruit pulp while adult flies have been reported feeding on various sources including extra-floral glandular secretions from plants, plant leachates, fruit juices, bacteria, honeydew and bird faeces in order to acquire sufficient carbohydrate and protein for survival and reproduction (Christenson and Foote 1960; Hendrichs and Hendrichs 1990; Manrakhan and Lux 2009; McQuate et al. 2003; Nishida 1958; Warburg and Yuval 1997). Studies on the mouthparts of adult *Bactrocera* and *Ceratitis* species have revealed that adult flies have a fluid-centered mode of feeding and a labellar-filter-feeding mechanism allowing them to ingest fluids and particles that are less than 0.5 μm in size (Vijaysegaran et al. 1997; Coronado-Gonzalez et al. 2008). All frugivorous female fruit flies are anautogenous, that is they need to feed on protein to realise their reproductive potential (Drew and Yuval 2001). Furthermore, nutrition plays an important role in both the regulation of oocyte maturation and male accessory gland development (Williamson 1989). Foraging behaviour of adult flies occurs at different hierarchical levels: the habitat (fruit-growing area), the patch (host trees or non-host trees) and the specific food item (Hassell and Southwood 1978; Prokopy and Roitberg 1989). The initial identification of a potential food item by a fly is largely achieved through olfaction (Dethier 1976). Olfactory receptors on the antennae and on the palps of fruit flies are sensitive to the gaseous products of amino acid breakdown, mainly ammonia (Rice 1989; Tsiropoulos 1992). The attraction of fruit flies to protein-based odours is exploited in the use of poisoned food baits for fruit fly control (Roessler 1989).

A thorough understanding of adult feeding behaviour has direct implications in optimising control of fruit fly pests using food baits (Hendrichs and Prokopy 1994). In relation to the application of food baits, knowing what attracts flies to food and understanding the factors that influence feeding behaviour can improve the efficacy of control strategies using food baits.

2.1 Ceratitis *Species*

Research on the feeding behaviour of *Ceratitis* species has largely been restricted to a few of the key pest species: the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann); *Ceratitis fasciventris* Bezzi; the Natal fruit fly, *Ceratitis rosa* Karsch; and the mango fruit fly, *Ceratitis cosyra* (Walker). Some of these fruit fly pests prefer to reside on host trees compared with non-host trees, and for this reason most of their food foraging activities are likely to occur within host patches (Manrakhan 2009; Hendrichs and Hendrichs 1990).

The type of food ingested influences survival and the reproductive activity of *Ceratitis* species. Survival of some pest species of *Ceratitis* was poor without a sugar source (Hendrichs and Hendrichs 1990; Hendrichs et al. 1991; Manrakhan and Lux 2006). Calling, mating, egg laying and egg fertility was greater in adult *Ceratitis* species feeding on a protein-rich diet than on a protein-poor diet (Kaspi et al. 2000; Kaspi and Yuval 2000; Papadopoulos et al. 1998; Manrakhan and Lux 2006; Taylor and Yuval 1999; Shelly et al. 2002; Hendrichs et al. 1991). The effect of protein on longevity of *C. capitata* varied amongst different studies. Some studies reported better survival of flies maintained on a constant diet of sugar and protein compared with flies maintained on only sugar sources (Cangussu and Zucoloto 1995; Manrakhan and Lux 2006). Other studies showed a reduced mortality in *C. capitata* flies when they were deprived of protein (Carey et al. 1998; Hendrichs et al. 1991; Kaspi and Yuval 2000).

Temporal patterns of feeding have been described for a number of *Ceratitis* species. With respect to time of the day, male *Ceratitis fasciventris* (Bezzi) and male *C. capitata* fed mainly in the morning and late afternoon respectively, after having engaged in reproductive activities (Hendrichs and Hendrichs 1990; Manrakhan and Lux 2006; Warburg and Yuval 1997). With respect to the age of flies, for *C. cosyra*, *C. fasciventris* and *C. capitata*, sugar consumption was greater soon after emergence whilst protein feeding usually occurred either in or after the first week of adult life depending on species and sex (Manrakhan and Lux 2009). Nutritional state had a significant influence on the responses of *C. cosyra*, *C. fasciventris* and *C. capitata* to food odours. Sugar deprivation increased responses of young flies to food odours but there was no preference for particular types of odours in young sugar-deprived flies (Cohen and Voet 2002; Manrakhan and Lux 2008). Protein deprivation in mature flies enhanced their response to protein odours (Barry et al. 2003; Manrakhan and Lux 2008; Prokopy et al. 1992). Not all protein odours are equally attractive to adult *Ceratitis* species. For example, amongst different animal droppings that form part of the natural food complex of *C. capitata*, a preference for droppings from birds and lizards compared with droppings from mammals was shown for this species (Prokopy et al. 1993). Moreover for *C. capitata* and other

Ceratitis species, natural food sources were more attractive than artificial food baits (Manrakhan and Lux 2008; Prokopy et al. 1992). Variation in fly responses to different artificial proteinaceous baits has also been recorded (Katsoyannos et al. 1999; Manrakhan and Kotze 2011). The degree of response to protein baits differed between *Ceratitis* species (Manrakhan and Kotze 2011); this has important implications as baits that are effective for control of one *Ceratitis* species may not be as effective for other *Ceratitis* species. Differences in responses to protein odours amongst *Ceratitis* species could be linked to their protein requirement and therefore their sensitivity to volatiles emanating from protein sources.

2.2 **Bactrocera** ***Species***

The three most important *Bactrocera* pest species in the African region include the oriental fruit fly, *Bactrocera dorsalis* (Hendel) previously known as *B. invadens* Drew, Tsuruta and White (Schutze et al. 2014); the peach fruit fly, *Bactrocera zonata* (Saunders); and the solanum fruit fly, *Bactrocera latifrons* (Hendel); they are all of Asian origin and only recently introduced in to the African region (De Meyer et al. 2014; Ekesi and Muchugu 2006). There is generally a lack of information on the feeding behaviour and food bait preferences of *B. zonata* and *B. latifrons*. In the island of Mauritius, investigations found that *B. zonata* responded equally well to a commercially available protein hydrolysate and processed brewery yeast waste (Gopaul et al. 2000). In contrast to most *Bactrocera* species, more information is available on the feeding behaviour of *B. dorsalis*. Early studies by Bess and Haramoto (1961) in Hawaii suggested that *B. dorsalis* foraged for food and shelter on plants other than one of its preferred host plants, guava. However, subsequent studies in Hawaii have shown that *B. dorsalis* prefers to forage on guava (Vargas et al. 1990). In laboratory studies under controlled conditions, *B. dorsalis* engaged in feeding behaviour during the morning (Arakaki et al. 1984). As with *Ceratitis* species, reproduction of *B. dorsalis* was affected by the type of food ingested. A protein source in the adult diet of *B. dorsalis* was important for reproduction (Shelly et al. 2005). For example, *B. dorsalis* males deprived of protein had fewer matings that those that had access to protein (Shelly et al. 2005). Protein feeding decreased attraction of mature adult *B. dorsalis* females to protein odours whilst immature protein-fed *B. dorsalis* females were equally attracted to fruit and protein odours (Cornelius et al. 2000). In studies conducted recently in Kenya, *B. dorsalis* showed preferences for particular protein baits, and females were more attracted to protein baits than males (Ekesi et al. 2014). In studies conducted in Hawaii, young female *B. dorsalis* had stronger positive responses to protein baits than older females (Barry et al. 2006; Pinero et al. 2011). The results of studies on food bait preferences for *B. dorsalis* have been at times conflicting. For example, in studies done in Tanzania and Kenya, the three-component Biolure (ammonium acetate, putrescine, trimethylamine) was less attractive to *B. dorsalis* than liquid protein baits such as Torula yeast (Ekesi et al. 2014; Mwatawala et al. 2006). However, current trials in South

Africa have found that the three-component Biolure is more attractive to *B. dorsalis* than liquid protein baits such as Torula yeast (Manrakhan et al., unpublished data). A more in depth understanding of the responses of *B. dorsalis* to food attractants is required for optimisation of monitoring and control efforts against this pest.

2.3 **Zeugodacus** *Species and* **Dacus** *Species*

In Africa, the melon fly, *Zeugodacus cucurbitae* (Coquillet) previously known as *Bactrocera cucurbitae* (Coquillet) (Virgilio et al. 2015) and a number of *Dacus* fruit fly species are economically important pests of vegetables in the family Cucurbitaceae (Ekesi and Muchugu 2006). Studies on a few cucurbit-infesting fruit fly pests have shown that flies preferred to congregate on non-host plants while host plants were only visited by gravid females for oviposition (Nishida and Bess 1950; Atiama-Nurbel et al. 2012). For this reason control efforts targeted at these species and based on food baits have been done on non-host plants rather than host plants (Prokopy et al. 2003). Other than studies on the distribution of cucurbit-infesting fruit flies within a habitat, there is very little information on their feeding behaviour. *Zeugodacus cucurbitae*; the lesser pumpkin fly, *Dacus ciliatus* (Loew); and *Dacus demmerezi* (Bezzi) respond to protein baits, although the degree of response differed between species and within some species in respect to age and starvation status depending on bait type (Barry et al. 2006; Deguine et al. 2012; Nestel et al. 2004; Pinero et al. 2011). There is a lack of information on the temporal feeding patterns of these species. Moreover, for some *Dacus* species, such as *D. ciliatus*, which do not respond well to commercially available protein baits (Deguine et al. 2012), detailed studies on their feeding requirements and habits are urgently required.

3 Mating Behaviour of African Fruit Flies

Afrotropical fruit flies, in particular those that are polyphagous, have complex mating systems which involve the formation of leks (Sivinski and Burk 1989). Leks are male communal display aggregations, with the purpose of attracting females (Sivinski and Burk 1989). An understanding of the mating behaviour of key African fruit fly pests is important in the development of SIT for control of these pests (Hendrichs et al. 2002). Male lures used for monitoring and control of African fruit fly species are known to influence the mating behaviour of some species (Khoo and Tan 2000; Shelly and Dewire 1994; Tan and Nishida 1998). The use of male lures in combination with insect growth regulators (IGRs) or pathogens will require a better understanding of the effect of these male lures on the mating behaviour of the flies since it is essential that lure-fed males interact and mate with wild females if sterilisation or transmission of pathogens is to be effective.

3.1 Ceratitis *Species*

The mating behaviour of *C. capitata* has been studied extensively over the years (see review by Eberhard [2000]). However, very little is known about the mating behaviour of other *Ceratitis* species. The courtship behaviour of *C. rosa*, *C. cosyra*, *C. fasciventris* and *Ceratitis catoirii* Guérin-Mèneville has been studied in laboratory and field cages (Manrakhan and Lux 2009; Quilici et al. 2002; Myburgh 1962). Unlike *C. capitata* and *C. catoirii* which are day mating species, *C. rosa*, *C. fasciventris* and *C. cosyra* began mating activity at dusk, staying in copula until day break (Manrakhan and Lux 2009; Quilici et al. 2002). In studies conducted under laboratory conditions in Kenya, protein in the adult food diet influenced the calling and mating behaviour of *C. fasciventris* and *C. cosyra* (Manrakhan and Lux 2006). Frequency of calling in *C. fasciventris* males, and mating in *C. fasciventris* and *C. cosyra*, was higher when the flies were fed on a protein-rich diet as compared to a protein-poor diet (Manrakhan and Lux 2006). For *Ceratitis* species other than *C. capitata*, the factors affecting their mating behaviour, remating habits and sperm transfer have yet to be elucidated. This lack of research on *Ceratitis* species other than *C. capitata* may be due to limited interest in developing SIT for control of those pests in Africa. However for other regions in the world which are still free of important polyphagous *Ceratitis* pests such as *C. rosa*, C. *cosyra* and *C. fasciventris*, the development of SIT targeting those species is still relevant and needs to be pursued since SIT can be used either as a preventative control measure against introduction of these pests, or as an eradication tool.

3.2 Bactrocera *Species*

Bactrocera species that are pests in the African continent are dusk-mating species, a characteristic of the majority of dacine fruit flies (Fletcher 1987). There is evidence for male-produced sex pheromones in *B. dorsalis* (Kobayashi et al. 1978). The rectal glands of male fruit flies produce and store sex pheromones (Fletcher 1987) and are present in male *B. dorsalis* (Schultz and Boush 1971). Sexually mature virgin *B. dorsalis* females were highly attracted to mature males and to the excised rectal glands of the males, particularly around dusk (Kobayashi et al. 1978). In *B. dorsalis*, mating begins at dusk when the light intensity falls to 280 Lux and continues until day break (Arakaki et al. 1984). Pairs of *B. dorsalis* remain in copula for ~10 h and copulation was found to be more successful in males that engaged in wing vibration (Arakaki et al. 1984). Under laboratory conditions adults only begin mating on the 11th day after emergence (Arakaki et al. 1984). Under field conditions, leks of 2–12 male *B. dorsalis* were found on host plants with each male defending an individual leaf; when a female arrived on a leaf the male mounts her and copulation proceeds (Shelly and Kaneshiro 1991). Female visits were not influenced by the sizes of leks suggesting a less intense female choice in the mating system of *B. dorsalis* compared with that of *C. capitata* (Shelly 2001). A different facet of female choice was demonstrated by Poramarcom and Boakes (1991), who showed that female *B. dorsalis* preferred dominant males and those that mated twice. Mating success was also greater in *B. dorsalis* males with previous exposure to methyl eugenol and protein (Shelly 2000; Shelly and Dewire 1994; Shelly et al. 2005; Tan and Nishida 1998). This may be because male *B. dorsalis* (reported as *Bactrocera papaya* Drew and Hancock in the publication) are known to convert methyl eugenol to other derivatives, particularly phenyl propanoids, which then act as sex pheromones to attract females during courtship (Hee and Tan 1998; Tan and Nishida 1998); one phenylpropanoid coniferyl alcohol was highly attractive to *B. dorsalis* females (Hee and Tan 1998).

Bactrocera latifrons, another important pest species in Africa, has a similar mating system to *B. dorsalis*. Jackson and Long (1997) described the mating behaviour of this pest species in field cages on coffee trees; leks of 4–9 calling males were observed and mating occurred between 1 h before sunset and 15 min after sunset (Jackson and Long 1997). *Bactrocera latifrons*, like other *Bactrocera* species, sequester male–specific attractants in their rectal glands (Nishida et al. 2009).

In contrast to *B. dorsalis* and *B. latifrons*, information on the mating behaviour of *B. zonata* is largely lacking. *Bactrocera zonata* males have a strong attraction to methyl eugenol (Tan et al. 2010). In the rectal glands of *B. zonata*, methyl eugenol is synthesised to form a blend of phenylpropanoid volatiles that are different to that produced by *B. dorsalis* (Tan et al. 2010).

3.3 **Zeugodacus** *Species and* **Dacus** *Species*

Zeugodacus cucurbitae is a dusk-mating species (Suzuki and Koyama 1980), similar to the *Bactrocera* pest species in Africa. Laboratory strains have shorter premating periods and initiate mating at higher light intensities than their wild counterparts (Suzuki and Koyama 1980). Lek formation has been suggested for *Z. cucurbitae* (Kuba et al. 1984; Kuba and Koyama 1985). Raspberry ketone (a derivative of Cuelure which is a known male lure of *Z. cucurbitae*) increased the production of female-attracting sex pheromone, male-aggregation pheromone and was also an allomone (Khoo and Tan 2000).

The mating behaviour of other cucurbit infesting fruit flies has been poorly studied. Rempoulakis et al. (2015) recently described the mating behaviour of *D. ciliatus* but the mating habits of the other *Dacus* species remain undescribed. For *Dacus* species that do not respond to commercially available protein baits, the use of male lures with toxins and pathogens as well as SIT could still be viable control tools. The development of these techniques will, however, require an in depth investigation of the mating behaviour of *Dacus* species.

4 Conclusion

Within the African fruit fly pest complex, feeding and mating behaviours have been elucidated for only a few species with a wider global distribution. For the remaining *Ceratitis*, *Bactrocera* and *Dacus* species with a limited worldwide distribution, there are still important knowledge gaps in their behavioural ecology. With horticulture expanding in Africa and increasing trade of horticultural produce from the region, it is important that these knowledge gaps are filled so that control methods can be optimised.

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