Active aggregation among sexes in bean flower thrips
(*Megalurothrips sjostedti*) on cowpea (*Vigna unguiculata*)

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Abstract

Male sexual aggregations are a common territorial, mating-related or resource-based, behaviour observed in diverse organisms, including insects such as thrips. The influence of factors such as plant substrate, time of day, and geographic location on aggregation of thrips is uncertain, therefore we monitored the dispersion of male and female bean flower thrips (BFT), *Megalurothrips sjostedti* (Trybom) (Thysanoptera: Thripidae), on cowpea, *Vigna unguiculata* (L.) Walp. (Fabaceae), over three cowpea growth stages and across three cowpea-growing areas of Kenya. Our results indicated that for all the crop growth stages, the density of BFTs varied over the time of day, with higher densities at 10:00, 13:00, and 16:00 hours than at 07:00 hours. Thrips densities did not differ among blocks at the budding stage, but they did at peak flowering and podding stages. Dispersion indices suggested that both male and female BFTs were aggregated. Active male aggregation occurred only on green plant parts and it varied across blocks, crop stages, and locations. Similarly, active female aggregation was observed in peak flowering and podding stages. Such active aggregation indicates a semiochemical or behaviour-mediated aggregation. Identification of such a semiochemical may offer new opportunities for refining monitoring and management strategies for BFT on cowpea, the most important grain legume in sub-Saharan Africa.

Introduction

Male aggregation is a common territorial and mating-related behaviour exhibited by avians, amphibians, mammals, and insects (Fiske et al., 1998). Such behaviour is typically classified as substrate-based, as observed in cicadas, tephritids, drosophilids, etc. Aerial-based aggregations are found among dipterans, such as chironomids, culcids, simuliiids, and ephemeropterans (Shelly & Whittier, 1997). Substrate-based aggregation behaviour of male thrips has been reported widely (Kirk, 1985; Olaniran & Kirk, 2012). Males of the genera *Thrips* and *Frankliniella* aggregate on corollas of flowers (Kirk, 1985; Milne et al., 2002). Over the past 20 years, aggregation behaviour has gained interest among thrips biologists (Kirk & Hamilton, 2004; Hamilton et al., 2005), leading to the identification of species-specific male-produced aggregation pheromones (Hamilton et al., 2005; Zhang et al., 2011; Akella et al., 2014) and contact pheromones (Olaniran et al., 2013).

The bean flower thrips (BFT), *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), is a key pest of grain legumes – especially cowpea, *Vigna unguiculata* (L.) Walp. (Fabaceae) – in sub-Saharan Africa (Tamo et al., 1993; Abate & Ampofo, 1996). It causes abscission of cowpea flowers resulting in significant yield losses of between 20 and 100% (Singh & Allen, 1980). The BFT also attack a wide range of alternative hosts mainly in the pea family (Fabaceae) (Tamo et al., 2002).

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Ecological studies on population dynamics over seasons have revealed that the BFT numbers greatly increase during specific crop growth stages, especially at flowering and podding (Ezueh, 1981; Salifu & Hodgson, 1987; Nyasani et al., 2013). However, prior to this study, in field surveys for thrips on grain legume crops such as dolichos, we noted that BFT males were highly aggregated. Many dolichos plants recorded very few or no males, whereas in very few dolichos plants high numbers of BFT males (sometimes up to 15 per plant) were observed (S. Subramanian, unpubl.). Based on this observation, we investigated the aggregation pattern among sexes of BFT on cowpea and assessed whether aggregation behaviour is active or passive and whether it is influenced by location, time of the day, crop growth stage, or plant part.

Materials and methods

Monitoring of male and female BFT densities on cowpea

Variation in male and female BFT densities in relation to time of day and crop growth stage was studied on a cowpea farm at the International Centre of Insect Physiology and Ecology (icipe) headquarters in Nairobi, Kenya.

Cowpea (var. Kakamega) was planted, after the land was ploughed, harrowed, and ridged. Planting was completed in March 2013 corresponding to the long rains season in Kenya. The farm (40° × 45 m) was divided into four planting date blocks (10 × 10 m) separated by a corridor of 0.5 m. In each block, planting was undertaken successively at 2-week intervals between May and June 2013 with intra- and inter-row spacing of 0.25 and 0.45 m, respectively. Standard agronomic practices were adopted (Dugje et al., 2009). Observations in each block with different planting dates were undertaken at three crop growth stages: budding (BD) (5 weeks after planting when mostly unopened buds and few first flowers were seen), peak flowering (PF) (8 weeks after planting when more than 90% of plants were flowering), and podding stage (PS) (10 weeks after planting when most of the plants had young pods with a few flowers). Within each crop growth stage, observations were taken on the number of male and female BFT for four consecutive sampling days. On each sampling date, 25 randomly selected cowpea plants were sampled at 3-h intervals, from 07:00 to 16:00 hours using the whole-plant tapping method. This involved tapping the plants gently for 5× on white enamel tray (25 × 45 cm) kept right below. The number of thrips which fell on the tray were quickly estimated (Pearson & Myers, 2000). Further samples of 10–25 flower buds based on the availability were randomly collected from different cowpea plants separated by a minimal distance of 2 m and placed in separate glass vials containing 70% ethanol for further observation of thrips in the laboratory. The sex of adult BFT emerging from flowers was identified and the total number of thrips per flower was recorded.

Assessment of bean flower thrips aggregation across cowpea-grown locations in Kenya

To understand the variation in aggregation of BFT across cowpea-grown locations, field observations were taken at podding stage in three provinces of Kenya: Nairobi province (Kasarani: 01.222S, 036.897E, and 1 602 m a.s.l.), Eastern province (Matuu: 01.160S, 037.530E and 1248.1 ma.s.l.), and Nyanza (Mbina: 00.431S, 034.208E, and 1140.0 ma.s.l.). In Matuu and Mbina, cowpea farms at podding stage were selected for sampling based on observations in the Nairobi field experiment. On each farm, observations on whole plants and flowers were taken at the same time and interval as described above. Four to nine replicated observations on 10–15 plants were taken depending on the farm size and density of BFT per plant. Thrips counts in Matuu and Mbina were compared with observations at the podding stage at Kasarani, Nairobi.

Statistical analysis

Analyses were performed using R v. 3.1.0 (R Development Core Team, 2014) using R Commander v. 1.6-3 (Fox et al., 2009) and Agricolae v. 1.1-4 packages (De-Mendiburu, 2013). To study the predictive factors for the number of BFTs, a negative binomial regression model was fitted because we had overdispersed count data as suggested by O’Hara & Kotze (2010). The likelihood ratio (LR) test strongly suggested that the negative binomial model was more appropriate than the Poisson model (LR test: P<0.0001). To start with, a full model including sex, block, stage, their interaction terms, and time of the day was fitted. The dispersion parameter for this model was 1.154 indicating that the data were overdispersed, meaning that the variability encountered in the data is not equal to the mean, as with the Poisson distribution. The negative binomial model was further fitted for each stage separately.

To study the thrips dispersion on plants and flowers, two indices were calculated: (1) Lloyd’s index of patchiness (LIP) (Lloyd, 1967) defined as

\[ LIP = 1 + \left( \frac{s^2 - \bar{x}}{\bar{x}^2} \right), \]

where \( s^2 \) represents sample variance and \( \bar{x} \) is the sample mean; and (2) variance-to-mean ratio (VMR). If LIP>1,
the population is considered aggregated and as LIP increases, the degree of aggregation also increases. If LIP = 1, then distribution is considered random. If LIP<1, the distribution is considered regular. To test whether the distribution was significantly different from that of a random population, a χ² test was performed for VMR.

**Table 1** Factors predictive for the presence of *Megalurothrips sjostedti* on cowpea plants at three crop stages, based on a negative binomial model

| Factor          | Budding              | Peak flowering             | Podding              |
|-----------------|----------------------|---------------------------|----------------------|
| **Time**        |                      |                           |                      |
| 07:00           | 1                    | 1                         | 1                    |
| 10:00           | 2.27 (1.31–3.95)     | 2.11 (1.48–3.05)          | 1.69 (1.30–3.76)     |
| 13:00           | 2.17 (1.24–3.83)     | 1.80 (1.25–2.60)          | 2.91 (2.25–2.72)     |
| 16:00           | 3.02 (1.76–5.24)     | 2.66 (1.87–3.80)          | 2.09 (1.60–0.86)     |
| **Sex**         |                      |                           |                      |
| Female          | 1                    | 1                         | 1                    |
| Male            | 4.12 (2.39–7.14)     | 0.65 (0.43–0.98)          | 0.61 (0.44–0.72)     |
| **Block**       |                      |                           |                      |
| 1               | 1                    | 1                         | 1                    |
| 2               | 1.15 (0.63–2.09)     | 0.63 (0.42–0.96)          | 0.51 (0.36–1.71)     |
| 3               | 0.98 (0.53–1.81)     | 0.84 (0.57–1.26)          | 1.24 (0.90–2.01)     |
| 4               | 0.76 (0.41–1.43)     | 0.71 (0.47–1.08)          | 1.46 (1.06–1.75)     |
| **Sex*block**   |                      |                           |                      |
| Female:block 1  | 1                    | 1                         | 1                    |
| Male:block 2    | 0.03 (0.01–0.08)     | 0.52 (0.26–1.02)          | 1.05 (0.63–0.97)     |
| Male:block 3    | 0.03 (0.01–0.08)     | 0.60 (0.32–1.12)          | 0.60 (0.37–0.73)     |
| Male:block 4    | 0.01 (0.002–0.06)    | 0.24 (0.11–0.52)          | 0.45 (0.27–0.001)    |

RR, risk ratio; CI, confidence interval; P-values are based on Wald tests.
using the expression
\[ x^2 = \left( \frac{s^2}{\bar{x}} \right) (\chi^2) = \left( \frac{s^2}{\bar{x}} \right) (N - 1), \]
with \((N - 1)\) degrees of freedom, where \(N\) is the number of observations (Hurlbert, 1990). In situations with aggregation, the cause of aggregation was determined (i.e., whether it was active – behaviour-mediated – aggregation or passive, influenced more by environmental factors). In this regard, the criteria outlined by Arbous & Kerrick (1951) were used to estimate the mean 'aggregation' size \(\lambda\) (Southwood & Henderson, 2000):
\[ \lambda = \frac{\bar{x}}{2k} v, \]
where \(\lambda\) is the mean number of individuals in the aggregation for the probability level allocated to \(v\), \(\bar{x}\) is the sample mean, \(k\) is the dispersion parameter obtained from the negative binomial model, and \(v\) is a function with \(\chi^2\) distribution with \(2k\) degrees of freedom. In interpreting \(\lambda\), we note that \(\lambda<2\) indicates that aggregation is more due to an environmental effect and not to active behaviour of the insect, whereas \(\lambda>2\) is an indication that the cause of aggregation is due to either factor, but especially active processes by the thrips (Salifu & Hodgson, 1987; Verghese et al., 1988). Field data collected in Matuu and Mbita were subjected to similar analyses. We used \(\chi^2\) tests to differentiate the proportion of male and female BFTs at each time of the day, block, and plant stage. All tests were performed with \(\alpha = 0.05\).

**Results**

**Density of male and female BFT on cowpea plants**

The mean number of male and female BFT by crop stages and time of the day are summarized in Figure 1A. As the sex-by-block-by-stage interaction term was significant in the full/initial model (LR test: \(P<0.0001\)), a negative binomial model was fit for each stage separately with time, sex, block, and sex-by-block in the model (Table 1). The results indicated that for all the stages, the sex-by-block interaction term was significant (\(P<0.0001\)), implying the densities of male and female BFT varied across the blocks (Figure 2A). After controlling for sex and blocks, time of the day was significantly associated with the density of BFT at all the plant stages and significantly more insects were collected at 10:00, 13:00, and 16:00 hours than at 07:00 hours (Figure 2B). Also, after controlling for time and block, it was four times more likely to get a male than a female BFT at the budding stage. At the flowering and podding stages, it was significantly less likely to get thrips as compared to females (Figure 2C).

**Density of BFT on cowpea flowers**

Negative binomial model results indicated that the difference in female densities per flower was not significant across block or time of day, whereas it differed across crop stages: female density per flower was higher at peak flowering (mean ± SE = 0.3 ± 0.1; \(Z = 2.3, P = 0.018\)) and podding (3.0 ± 0.4; \(Z = 2.7, P = 0.006\)) than at budding (0.1 ± 0.0). At all observation times, males were mostly absent in flowers over the crop growth stages (Figure 1B).
Overall, the density of BFT varied across the three locations in Kenya. Male numbers per plant were much higher in Mbita (mean ± SE = 36.2 ± 2.9; Z = 8.1, P < 0.0001) than in Nairobi (1.3 ± 0.1) or Matuu (0.4 ± 0.1). Similarly, female numbers per plant were higher in Mbita (7.7 ± 0.5; Z = 8.9, P < 0.0001) than in Nairobi (2.7 ± 0.1) or Matuu (3.3 ± 0.2). Male BFT densities were lower than female densities in Matuu (Z = −14.2, P < 0.0001) or Nairobi (Z = −9.17, P < 0.0001). In Mbita, male BFT densities were higher than female densities (Z = 16.9, P < 0.0001).

Dispersion indices indicated that in all the locations, both male and female LIPs were significantly higher than 1 (Table 4). Male LIPs were always higher than female LIPs. In the field, the values of λ for both male and female BFT were >2 in Mbita and Nairobi only. As earlier noted in Nairobi, although males were occasionally spotted on green plant parts, they were mostly seen on the leaves (Figure 3A); flowers of cowpea were mostly populated with female BFT (Figure 3B).

**Discussion**

Previous studies of *M. sjostedti* have revealed that at higher densities the adults are highly aggregated (Salifu & Hodgson, 1987), which is suggestive of aggregation behaviour. However, beyond this indication and to the best of our knowledge, no detailed studies on aggregation in sexes of BFT or on factors associated with such aggregated dispersion are available in the literature. Female BFT occur in cowpea flowers in low numbers during the budding stage, but increased with the crop growth stage. Several authors have revealed that at higher densities the adults are highly aggregated (Salifu & Hodgson, 1987), which is suggestive of aggregation behaviour. However, beyond this indication and to the best of our knowledge, no detailed studies on aggregation in sexes of BFT or on factors associated with such aggregated dispersion are available in the literature. Female BFT occur in cowpea flowers in low numbers during the budding stage, but increased with the crop growth stage. Several authors

**Table 2**  Crowding indices for male and female *Megalurothrips sjostedti* by crop stage and block

| Crop stage  | Block | LIP | VMR | χ² | P           | λ     | d.f. | P     | λ    |
|-------------|-------|-----|-----|-----|-------------|-------|------|-------|------|
| Budding     | 1     | 8.9 | 17.81 | 1923.1 | <0.0001 | 3.68 | 1.5 | 1.21 | 131.2 | 0.0640 | – | 108 |
|             | 2     | 0.2 | 0.95 | 102.0 | 0.6200 | – | 1.7 | 1.32 | 141.7 | 0.0140 | 1.81 | 107 |
|             | 3     | 8.4 | 1.36 | 136.4 | 0.0091 | 0.09 | 1.3 | 1.14 | 114.4 | 0.1500 | – | 100 |
|             | 4     | 0.5 | 0.99 | 101.0 | 0.5100 | – | 2.9 | 1.65 | 168.1 | <0.0001 | 1.02 | 102 |
| Peak flowering | 1     | 4.5 | 3.60 | 360.0 | <0.0001 | 1.62 | 1.4 | 1.48 | 147.7 | 0.0014 | 4.26 | 100 |
|             | 2     | 4.9 | 1.95 | 192.7 | <0.0001 | 0.62 | 1.5 | 1.37 | 136.0 | 0.0080 | 2.73 | 99 |
|             | 3     | 6.6 | 3.12 | 309.4 | <0.0001 | 0.90 | 1.6 | 1.57 | 154.9 | 0.0003 | 3.61 | 99 |
|             | 4     | 1.4 | 1.05 | 101.2 | 0.3400 | – | 1.9 | 1.66 | 159.5 | 0.0001 | 2.89 | 96 |
| Podding     | 1     | 4.3 | 6.85 | 678.5 | <0.0001 | 4.18 | 2.1 | 3.92 | 388.4 | <0.0001 | 7.85 | 99 |
|             | 2     | 3.6 | 3.38 | 334.3 | <0.0001 | 2.37 | 2.1 | 2.35 | 232.9 | <0.0001 | 3.83 | 99 |
|             | 3     | 2.7 | 3.13 | 309.9 | <0.0001 | 2.94 | 1.3 | 1.91 | 189.4 | <0.0001 | 11.60 | 99 |
|             | 4     | 3.0 | 3.23 | 319.4 | <0.0001 | 2.84 | 1.5 | 3.09 | 306.4 | <0.0001 | 14.63 | 99 |

LIP, Lloyd’s index of patchiness; VMR, variance-to-mean ratio; λ, estimated number of individuals in the aggregation.

**Table 3** Dispersion indices of female *Megalurothrips sjostedti* on cowpea flowers

| Crop stages | LIP | VMR | χ² | d.f. | P | λ |
|-------------|-----|-----|-----|------|---|---|
| Budding     | 1.3 | 1   | 273.7 | 265 | 0.3000 | – |
| Peak flowering | 2.2 | 1.4 | 233.9 | 165 | 0.0003 | 1.4 |
| Podding     | 1.8 | 3.3 | 492.3 | 149 | <0.0001 | 12.8 |

LIP, Lloyd’s index of patchiness; VMR, variance-to-mean ratio; λ, estimated number of individuals in the aggregation.
have observed such increase in BFT population from the initial infestation at the budding stage (macroscopic flower buds to anthesis) to full infestation at later flowering and podding phases (Ezueh, 1981; Salifu & Hodgson, 1987; Salifu & Singh, 1987). Recently, Niassy et al. (2013) also observed that BFT population on French bean, *Phaseolus vulgaris* L., was significantly lower before flowering than after. Our observation concurs with their findings and provides additional information with regard to sex-specific differences in infestation of cowpea growth stages.

We also found out that both male and female BFT infested the green plant parts of the cowpea crop, whereas flowers were only infested by females. The density of BFT on plants differed across blocks, crop growth stage, and time of day. Although both sexes presented aggregation patterns, males were more aggregated than females and aggregations were mainly observed on the green plant parts, especially the leaves. Similar aggregation of males on terminal leaves were also observed in *Pezothrips kellyanus* Bagnall (Mound & Jackman, 1998; Mound, 2004; Navarro-Campos, 2013). However, previous reports on male aggregation of other thrips species indicated that it takes place mainly on the corolla of flowers (Kirk, 1985; Terry & Dyreson, 1996). Frequent mating behaviour by *P. kellyanus* on ripe citrus fruits has been reported to occur during the late afternoon around 17:00 hours (Webster et al., 2006).

Generally, females were observed in flowers and their numbers significantly increased from budding to podding stages. This could be for feeding or oviposition, as reported in BFT and other thrips (Childers & Achor, 1995; Gahukar, 2004). In addition to higher LIP values observed in both sexes, the mean ‘aggregation’ size $\lambda$ values were >2, indicating active aggregation of both male and female, as suggested by Salifu & Hodgson (1987) and Verghese et al. (1988). Our results also reveal that factors such as block, crop growth stage, and location could influence BFT aggregation behaviour. In many thrips species, similar aggregations have been ascribed to the possibility of a semiochemical-mediated interaction between the sexes (Mound & Jackman, 1998; Milne et al., 2002). Aggregation pheromones responsible for such behaviour in thrips species such as *Frankliniella occidentalis* (Pergande) (Kirk & Hamilton, 2004; Hamilton et al., 2005), *Frankliniella intonsa* (Trybom) (Zhang et al., 2011), and *Thrips palmi* Karny (Akella et al., 2014) have been identified. The active aggregation observed in this study and recent report on the presence of male sternal glands associated with pheromone production in BFT (Krueger et al., 2015), underlines the need to identify possible pheromones associated with BFT aggregations.

### Table 4 Dispersion indices of male and female *Megalurothrips sjostedti* on cowpea at Matuu, Mbita, and Nairobi (Kenya)

| Location  | LIP  | VMR  | $\chi^2$ | P       | $\lambda$ | LIP  | VMR  | $\chi^2$ | P       | $\lambda$ | d.f. |
|-----------|------|------|----------|---------|-----------|------|------|----------|---------|-----------|------|
| Matuu     | 5.7  | 3.1  | 537.9    | <0.0001 | 0.79      | 1.3  | 1.9  | 330.2    | <0.0001 | 0.00      | 175  |
| Mbita     | 2.9  | 70.9 | 21477.3  | <0.0001 | 91.76     | 2    | 8.4  | 2555     | <0.0001 | 23.25     | 303  |
| Nairobi   | 3.8  | 4.55 | 1816.8   | <0.0001 | 3.14      | 1.8  | 3.17 | 1264     | <0.0001 | 7.28      | 399  |

LIP, Lloyd’s index of patchiness; VMR, variance-to-mean ratio; $\lambda$, estimated number of individuals in the aggregation.

![Figure 3](image.png)

**Figure 3** Aggregation of male and female *Megalurothrips sjostedti* on cowpea at the podding stage. (A) Males (slender and light coloured) on a leaf, (B) females (robust and black) on a flower.
Sexual communication in a diverse array of phytophagous insects is strongly influenced by host plant chemistry (Landolt & Phillips, 1997). The increase in BFT populations as determined by cowpea growth stage, and the aggregation of males and females in leaves and flowers suggest interactions between host plant cues and pheromones which need to be investigated. The densities of adult BFT varied with time of day with more insects collected at 10:00, 13:00, and 16:00 hours than at 07:00 hours. This variation could be attributed to variation in temperature and time of the day, which also affect flower opening and closing in the host plant (Ekesi et al., 1999; Ige et al., 2011).

Among the three cowpea-growing areas, higher numbers of BFT, especially males with higher aggregation indices, were observed at Mbita than at Nairobi or Matuu. This difference could be ascribed to the lower altitude in Mbita, with higher temperature and higher humidity (Murage et al., 2012), which are among the preferred growth conditions for BFT and its host (Bottenberg et al., 1997; Ekesi et al., 1999).

Aggregation of sexes in BFT may be influenced by factors including crop growth stage, time of day, and biogeographical parameters. However, further research should focus on defining factors associated with this aggregation, such as mating/defence behaviour (Terry & Dyreson, 1996), role of male aggregation pheromones (Milne et al., 2002; Hamilton et al., 2005), and their interaction with plant growth stages (Sampson & Kirk, 2013). Defining the factors associated with the aggregation and identification of such aggregation pheromones may aid in refining monitoring strategies for BFT and in appropriate timing of management interventions.

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