Insect. Soc. (2016) 63:243–248
DOI 10.1007/s00040-015-0456-9

Insectes Sociaux

RESEARCH ARTICLE

Nuptial flights behavior of the African weaver ant, *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae) and weather factors triggering flights

W. A. Nene[1] · G. M. Rwegasira[1] · M. G. Nielsen[2] · M. Mwatawala[1] · J. Offenberg[2]

Received: 11 May 2015 / Revised: 22 November 2015 / Accepted: 23 November 2015 / Published online: 9 January 2016

Abstract Weaver ants (*Oecophylla* spp.) are intensively studied in basic and applied contexts. Yet, little is known about their mating behavior. Knowledge on their reproductive strategy is a prerequisite to the basic understanding of their life history and may provide valuable information facilitating their use in integrated pest management (IPM) and protein production (entomophagy). Here, we report on the behavior displayed by *O. longinoda* in relation with their nuptial flights in Tanzania and test for environmental cues that may trigger the flights. Based on observations of 56 flights recorded over 2 years, we found that sexuals aggregate on nest surfaces prior to flights. We also found that flights took place during the raining season, and all flights took place in evenings just before sunset. Further to these, days with flights were associated with higher relative humidity and less sun shine compared to days without flights. Also, flights mainly took place around full moons. However, this correlation was based on a total of only five full moon phases and should, therefore, be interpreted with caution. The results also showed that flights were only significantly correlated with weather parameters during the early part of the mating season, the trend changed thereafter probably due to depletion of sexuals in the nests as the season progressed. This information improves our understanding of ant nuptial flights and offers a tool to improve forecasts of *O. longinoda* flights, enabling easier collection of mated queens to stock ant nurseries that supply ant colonies for IPM-programs.

✉ W. A. Nene
wilsoninene@gmail.com

[1] Department of Crop Science and Production, Sokoine University of Agriculture, Box 3005, Morogoro, Tanzania

[2] Department of Bioscience, Aarhus University, Århus, Denmark

Keywords African weaver ant · Sexuals · Nuptial flight · Weather · Entomophagy · Tanzania

Introduction

Mating is the key process of reproduction. Most ant species mate during or after nuptial flights, where males and queens (sexuals) liberate from their natal nests to find mating partners from other colonies (Kaspari et al. 2001; Depa 2006; Levin et al. 2008; Peeters and Molet 2010; Gomez and Abril 2012). The copulation between unrelated sexuals (Depa 2006) provides an opportunity for genetic mixing and is an important part of the life history of most ant species (Dhami and Booth 2008). Therefore, observations on the behavior of ants in relation to their nuptial flights are of basic interest and could bring a broader understanding of ant life histories and ecology (Dunn et al. 2007).

To ensure genetic mixing, it is crucial that conspecific ant colonies are able to time their flight with neighbouring colonies. This requires either communication between colonies or some common flight triggers. Weather parameters have been suggested to trigger the flights of several ant species (Depa 2006; Gomez and Abril 2012). For example, the mating flight of *Pheidole sitarches* was reported to take place on days with moderate rain and an overcast sky (Wilson 1957). Kaspari et al. (2001) indicated that temperature and rainfall were abiotic factors of importance when several ant species were timing their flights in the Neotropics. The swarming behavior of the species, *Atta vollenweideri* FOREL is highly associated with rainfall and a temperature increase (Staab and Kleineidam 2014). Further, Dhami and Booth (2008) indicated that the nuptial flight of *Solenopsis invicta* generally occurred after one or

2 days of rain and at temperatures between 21–33 °C and RH of above 80 %.

In the case of the two extant *Oecophylla* species (*O. smaragdina* and *O. longinoda*), mating behavior is not only of basic interest, but also important in an applied context. These ants are used in biological control programs in the tropics where they protect crops against pests, resulting in increased crop yields and/or higher fruit quality (Way and Khoo 1992; Barzman et al. 1996; Peng and Christian 2007). Furthermore, they may be utilized as protein food (Sribandit et al. 2008; Offenberg 2011; FAO report 2013) or feed (Cesard 2004) and in this way contribute to food security (Offenberg and Wiwatwitaya 2009). In both types of utilization, it is important for farmers to obtain right queen colonies, but it can be difficult to find the maternal queen in wild colonies (Peng et al. 1998). Therefore, ant nurseries, where live ant colonies can be reared, are under development (Rwegasira et al. 2014). Ant nurseries need to collect newly mated queens' right after their nuptial flight to stock the production of larger colonies (Rwegasira et al. 2015). A reliable prediction of *Oecophylla* mating flights via identification of weather based triggers may reduce the costs of collecting such queens.

The mating season of *Oecophylla* spp. has been reported to coincide with rainy seasons (Way 1954; Vanderplank 1960; Offenberg and Wiwatwitaya 2010; Peng et al. 2013; Rwegasira et al. 2015), and studies on *O. smaragdina* showed that their mating flight takes place early in the morning (Renkang Peng, unpublished data). However, the timing of flights in *O. longinoda* had never been reported. Moreover, there exists little knowledge about the mating behavior of *O. longinoda*. Weather parameters have long been suggested to trigger *O. longinoda* mating flights but specifics on which parameters and to what extent have never been elucidated. Whether the flights occur at a limited part of the day as seen in *O. smaragdina* or extended across range of time over the day had never been established.

In the present study, we observed the mating behavior and the timing of the nuptial flight of *O. longinoda*. In particular, we tested for correlations between weather parameters and nuptial flights and did extensive observations to identify the time of the day when flights occur. The presented results have improved our understanding of weaver ant life history and ecology and they provide a tool to predict *O. longinoda* flights, making the collection of queens for ant nurseries easier, cheaper and more reliable.

Materials and methods

Study area

Studies were conducted at Naliendele Agricultural Research Institute (NARI) (10°21′22.49″S, 40°09′57.05″E and 140 m above sea level) about 10 km from Mtwara town in the southern part of Tanzania. The Mtwara region has a unimodal wet season, with regular rains from November/December to April/May. The annual rainfall ranges from 810 to 1090 mm. Mating behavior and flight events were recorded by visual inspection and by two web cams. The study period covered 2012/13 and 2013/14 mating seasons, and included 25 colonies (18 colonies under visual observations in fields and 7 colonies on close observation under webcam).

Timing of nuptial flights

Two cameras (IP Edimax Camera; Edimax Technology Co., Ltd) were placed close to nests to monitor flight events from December, 2013, to the end of February, 2014 (during the second season of observation). The cameras focused on nests of seven ant colonies kept on potted mango and cashew seedlings, set on tables outside a residential house, for easy surveillance and security. The colonies were introduced 3 months prior to monitoring, to allow for nest building and establishment. One camera focused on a single nest at a time, and the second camera monitored at least six nests at a time. The focuses of the cameras were turned to other nests after the release of sexuals. The cameras recorded timing of preparation for and occurrence of flights.

Pre- and post-flight behavior on nests

Colonies containing mature sexuals, i.e., imago winged males and winged queens with green gasters, were identified and selected for monitoring. Two colonies were monitored in situ at sunrise (between 06:30 a.m. and 08:30) and sunset (from 03:00 to 06:30 p.m.) during the first mating season. Preliminary records showed increased levels of nest surface activity during these times. Another 25 colonies, located at three sites approximately 1 km apart, were monitored in the evenings only during the second season.

During monitoring, we estimated the number of males and queens aggregating on the outside surfaces of the nests and; the numbers dispersing from the nests on days when flights occurred. We also recorded (on flight days) the duration of each aggregation, as the time between occurrence of first two sexuals and departure of all sexuals from the nest surface and; the duration of each take off event as the time between taking off of the first and the last sexual.

Finally, we compared the number of sexuals aggregating on nest surfaces; number of sexuals aggregating in the mornings between days with and without flight in the following evenings and number of sexual aggregating in the evenings on days with and without flight; the duration of aggregations and take off between small and large flights (small flights occurred when less than 50 sexuals dispersed per colony and big flights occurred when at least one colony released more than 50 sexuals). We also determined whether ants abandoned or continued to occupy the nests after the release of sexuals. The presence of workers and the physical condition of the nests were recorded 3 days after a flight had taken place. As data were not normally distributed and without variance homogeneity, statistical comparisons were based on non-parametric Mann–Whitney tests performed with GenStat software.

Association of weather parameters and mating flights

Occurrences of mating flights were closely monitored on six nests in each of the 18 ant colonies containing mature sexuals, from November to March, 2013/14. Monitoring was done in the evenings, when mating flights occur. Weather data were collected from the Tanzania Meteorological Agency (TMA) at Mtwara airport located approximately 3 km from the experimental sites. Daily total rainfall, daily average temperature, average minutes with sunshine per hour of the day, average wind speed, daily average relative humidity, cloud cover and average air pressure were collected. Additionally, moon phase was recorded as the percentage of the moon visible on a particular day (disregarding cloud cover).

We recorded flight days (days with at least one flight) in both seasons. One flight was recorded when at least one nest in the colony released sexuals. Thus two flights were recorded if nests from two different colonies released sexuals. Monitoring periods were divided into days with small flights and days with at least one big flight.

Logistic regression analysis was used to determine association between weather parameters/moon visibility and occurrence of nuptial flights. Also logistic regression was performed to determine the relationship between male aggregations in evenings and occurrence of nuptial flight. Data were analysed using JMP 11.1.1 software.

Results

Timing of nuptial flights

We recorded 56 mating flights in 25 ant colonies during the study period, of which 15 and 41 occurred in the first and second season, respectively. We also recorded 28 flight days, 11 in the first season and 17 in the second season. In some cases, flights occurred from several colonies on the same day. In addition, we recorded 25 flights using cameras that focussed on seven colonies kept outside a residential house during the second season. The remaining flights were recorded visually in the field. Of all 56 flights, 54 (96.4 %) started between 18:25 and 19:00 hours, whereas only two flights (3.6 %), started between 17:00 and 18:00 hours. At no other time of the day were any flights observed.

Throughout the mating season, males aggregated on the outside of the nest surface in the mornings and evenings only, even on days without flights. Queens were almost exclusively seen on nest surfaces on days with flights (see below). Queens aggregated 3–7 min before the start of the take off. No aggregation was recorded by cameras during other periods of the day.

Pre- and post-flight behavior on nests

On days with flights, there were unusually high activities of workers as well as males and queens on nest surfaces and on the leaves near the nests, 1–2 min before the first sexuals took off. More than 90 % of the flights happened from nests composed of old leaves. Due to the hectic movements in and out of the nests, the entry holes expanded and increased, and the silk between leaves were broken. Workers were observed to escort the sexuals for the take off.

About 3.7 times more males aggregated in the evenings, on days with flights compared to days without flights. There was no significant difference on number of males that aggregated in the mornings between days with and without flights on the following evenings (Table 1). Queens did not aggregate on nest surfaces in the mornings and showed almost no aggregation on evenings without flights. However, queens aggregated in the evenings with flights (Table 1)

Male aggregations lasted longer on days with big flights than days with small flights, but the flight event itself was shorter (Table 2). More than 80 % of the nests from which

Table 1 Numbers of aggregating males and queens on days with and without flights

	Mean (SE), n		Test statistic
	Days with flights	Days without flights	
Number of males aggregating in the evenings	135.8 (34.5), **5**	36.9 (4.7), **35**	Mann–Whitney test, $U = 14$, $p < 0.001$
	Days with flight in the evening	Days without flight in the evenings	
Number of male aggregating in the mornings	19.0 (4.5), **5**	11.3 (1.2), **35**	Mann–Whitney test, $U = 47.0$, $p = 0.099$
	Evenings with flight	Evenings without flight	
Number of queens aggregating	47.0 (38.3), **5**	0.91 (0.11), **35**	Mann–Whitney test, $U = 4.5$, $p < 0.001$

Bold values indicate the total number of colonies

Table 2 Duration of male aggregation and take off duration in relation to the size of flights

	Mean (SE), n	Days	Test statistic
	Days with big flights	Days with small flights	
Duration of males aggregation (min)	88.1 (5.09), **22**	28.2 (1.50), **14**	Mann–Whitney test, $U = 4.5$, $p < 0.001$
Take off duration (min)	12.1 (2.0), **23**	19.2 (1.4), **18**	Mann–Whitney test, $U = 4.5$, $p < 0.01$

Bold values indicate the total number of colonies

flights occurred were abandoned within 3 days after the flight. The abandoned nests were in a bad condition, with large holes in the silk constructions.

Relationship between weather parameters/moon visibility and mating flights

Our results showed that days with flights had higher relative humidity, higher percentage of the moon visible and fewer hours of sunshine (Fig. 1a–c). A unit increase in relative humidity increased the probability of flight occurrence by 12 % (exp (β) = 1.12; $p = 0.03$), while a unit increase in percentage moon visible significantly increased the likelihood of flight occurrence by 2 % (exp (β) = 1.02; $p = 0.02$) (Table 3). However, an increase in sunshine hours during the day, significantly decreased the likelihood of predicted flights (exp (β) = 0.97; p 0.05). Results in Table 3 showed that, rainfall, air pressure, temperature, wind speed and cloud cover had no effect on occurrence nuptial flight for *O. longinoda.*

Furthermore, increase in relative humidity on 2 or 1 day before the flight significantly increased the likelihood of flight to take place (Table 4). Additionally, flight was significantly associated with increase in relative humidity, increase in cloud cover and decrease in sunshine hours in a day after the nuptial flight (Table 4).

Finally an increase in male aggregation in the evening was significantly associated with occurrence of nuptial flight exp ((β) = 1.04, $p = 0.02$).

Discussion

Our results showed that flights take place just before sunset. Assessment of occurrence of flights should, therefore, be done in the evenings. Also, searches for mated queens should ideally take place during nights or mornings after flights, before too many queens fall prey to natural enemies. Results also signify that since flights occur at nearly sunset, light trapping may be used as a means to collect queens as previously suggested (Rwegasira et al. 2015). This information will facilitate collection and trapping of newly mated queens for rearing in ant nurseries. Time of flight for *O. longinoda* is in contrast to a closely related *O. smaragdina*, which are known to fly at sunrise (Peng et al. 2013).

As with many other ant species, *O. longinoda* started their mating flights first; by aggregations of males around nest openings, followed by aggregations of queens soon after. Following aggregations, sexuals took off from the nests but the actual mating was not observed in this study. Males aggregated both in mornings and in evenings, but they only flew in the evenings, where aggregations were also more pronounced. It is puzzling that males aggregated but never flew in the morning. We hypothesise that evening flights are a trait derived from original morning flights and that morning aggregations are a relic from this earlier behavior. The closely related *O. smaragdina* fly at sunrise (Peng et al. 2013).

We found that on days with big flights, durations of aggregations were longer, but the durations for taking off of sexuals from the nests were shorter. As more traffic of sexuals is needed on days with big flights, aggregations may last longer. The take off period, on the other hand, may be shorter as the stimuli may be strong on such days. This effect may further be reinforced if already dispersing sexuals use pheromone calls to stimulate more individuals to join the flight, as this would further shorten hesitation time.

The aggregation behavior displayed by sexuals on the nests may also inform ant collectors about the probability of a flight. If more than usual number of males or queens aggregate on nest surfaces in the evening, then a flight is likely to take place, and therefore queens should be collected during the night or the next morning.

The present study showed that periods within the mating season with less sunshine and high relative humidity increased the probability of mating flight to take place. As also observed among other ant species, weather parameters were associated with flight events (Staab and Kleineidam 2014). Days before, with, and after flights were all associated with high humidity, which may be adaptive for founding queens as they and their initial brood are in the early phase of colony founding, fully exposed to the environment and may suffer desiccation. Not until the first larvae reach the last instar can they produce the silk needed to construct a nest that can protect the founding colony against desiccation (Hölldobler 1983). Thus, incipient colonies are especially prone to desiccation in the period immediately following the mating flight. This is also supported by lower sunshine hours in flight day, higher cloud cover and lower sunshine hours found on days following a flight. It was observed that if wind increased during male aggregations, the workers started to escort males back into the nests. The low wind speed on days with flights may also be adaptive, as the sexuals may not be strong fliers and may

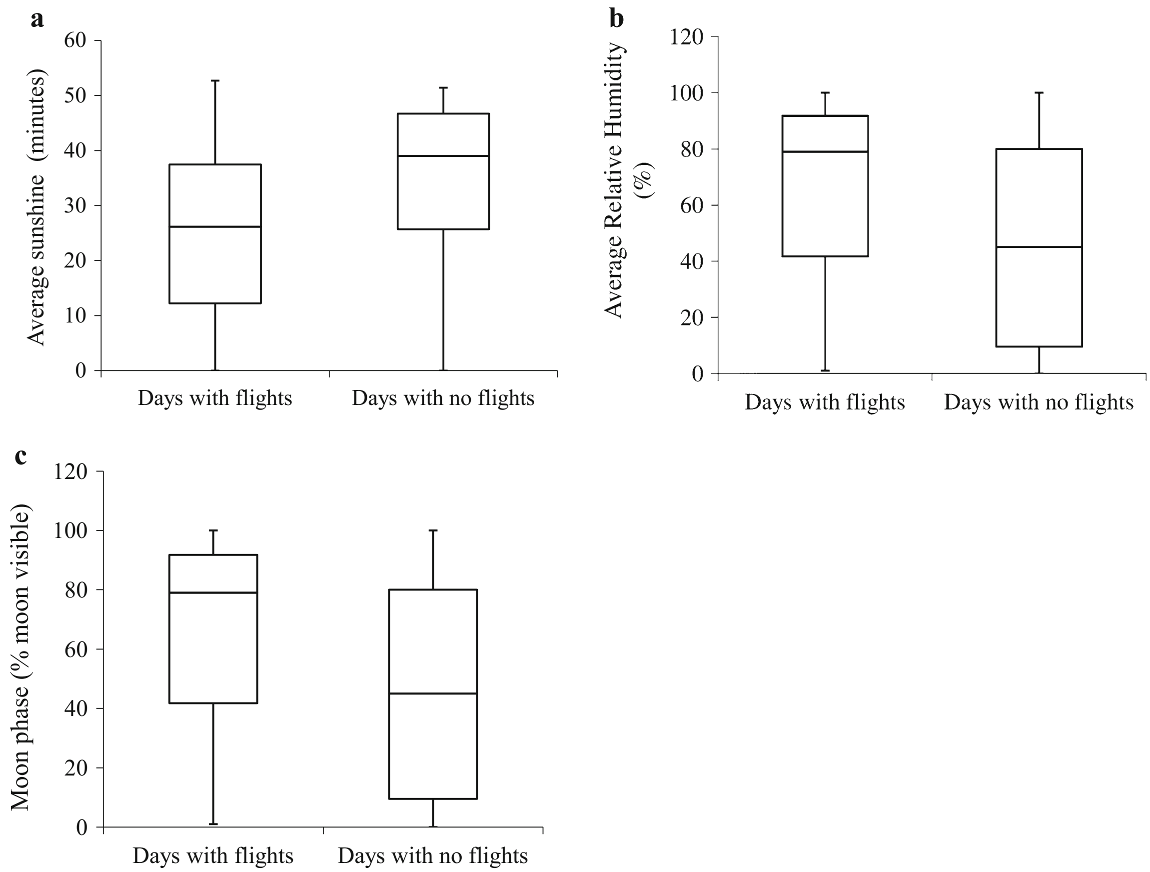

Fig. 1 Box plots showing relationships of; **a** sunshine (average minutes per hour of the day), **b** relative humidity and **c** moon phase, between days with and without mating flights. *N* and *p* values are given in Table 3

Table 3 Logistic regression results showing relationship between weather parameters/moon phase for *O. longinoda* nuptial flights at Naliendele, Tanzania

Parameters	Estimates	Std err	(χ^2)	Prob.	Exp (β)
%Moon visibility	0.017	0.007	5.54	0.02	1.02
Average sunshine hours	−0.028	0.014	3.75	0.05	0.97
%Relative humidity	0.109	0.050	4.68	0.03	1.12
Rainfall (mm)	0.012	0.009	1.76	0.18	1.01
Cloud cover	−0.003	0.170	0.00	0.98	0.99
Wind speed m/s	−0.141	0.161	0.77	0.38	0.86
Air pressure	−0.224	0.134	2.80	0.09	0.79
Temperature (°C)	−0.207	0.210	0.98	0.32	0.81

The analysis in Table 3 compared days during mating season which included 22 and 91 days with and without flights, respectively

need calm conditions if males use pheromones to call the queens as seen in other species (Peeters and Molet 2010).

In the present study, flights were not correlated with air pressure or rain. This is in contrast to *O. smaragdina*, where

Table 4 Influence of weather parameters on *O. longinoda* nuptial flights

Days before and after a flight day	Parameters	Estimates	Std err	(χ^2)	Prob.	Exp (β)
Two days before a flight	%Relative humidity	0.103	0.037	7.50	0.006	1.108
One day before a flight	%Relative humidity	0.112	0.050	4.87	0.027	1.118
One day after a flight	%Relative humidity	0.076	0.037	4.26	0.038	1.078
	Sunshine hours	−0.035	0.015	5.42	0.019	0.965
	Cloud cover	0.314	0.124	6.38	0.011	1.368

Weather parameters showing significant differences between days up to (1 and 2 days before a flight and 1 day after a flight) compared to all other days during mating season excluding flight days. The analysis included only weather parameters which showed significance differences. Probabilities (Prob.) are based on Logistic regression analysis under Generalized Linear Model. In this analysis, there were 22 and 91 days with and without flights, respectively flights were highly associated with days with high air pressure and no rain (Nielsen et al. unpublished data). However, the two species fly at different times of the day, with different weather parameters.

Interestingly, flights were also associated with full moon periods. In contrast to *O. smaragdina*, *O. longinoda* fly in the evenings. Thus, the newly mated queens must search for suitable nesting sites during the night, probably with the aid of moonlight, explaining why flights are related to full moon phases. In another study, *Oecophylla* ants showed profound visual orientation (Dejean 1990). The association between flight and full moon must, however, be taken with caution as the observed flights only covered a total of five full moon phases in the two seasons. As such, more observations covering more moon phases would be required for a more robust statistical analysis.

Combining the information given above may provide ant queen collectors with a tool to fine-tune their forecasts of mating flights for a more or less precise timing hence more efficient and effective collections. This will save time and costs, resulting in a cheaper production of *O. longinoda* colonies. This again may facilitate the implementation of the use of weaver ants in biocontrol programs and protein production (Offenberg 2011, 2015).

Acknowledgments We thank the Danish International Development Agency (Project DFC 10-025 AU) for financially supporting this study. Naliendele Agricultural Research Institute and farmers at Naliendele village are acknowledged for providing the fields for the experiments. Our sincere gratitude is to Mr. Hasan Libubulu and Frank Thadeo for their assistance in data collection.

References

Barzman MS, Mills NJ, Cuc NTT (1996) Traditional knowledge and rationale for weaver ant husbandry in the Mekong Delta of Vietnam. Agric Hum Values 13:2–9

Cesard N (2004) Forest products livelihoods and conservation. Case studies of non-timber forest products systems. Center for International Forest Research, Jakata, Indonesia

Dejean LA (1990) Circadian rhythm of *Oecophylla longinoda* in relation to territoriality and predatory behavior. Physiol Entomol 15:393–403

Depa L (2006) Weather condition during nuptial flight of *Manica rubida* (Latreille, 1802) (Hymenoptera formicidae) in Southern Poland. Myrmecol News 9:27–32

Dhami and Booth (2008) Review of dispersal distances and landing site behaviour of *Solenopsis invicta* Buren, Red Imported Fire Ant (RIFA). http://www.biosecurity.govt.nz/files/pests/invasive-ants/red-imported-fire-ants/rifa-dispersal-distances-landing-site-behaviou. Accessed 17 Sept 2013

Dunn R, Parker CR, Geraghty M, Sanders NJ (2007) Reproductive phenology in a diverse temperate ant fauna. Ecol Entomol 3:135–142

FAO report (2013) Edible insects: future prospects for food and feed security. FAO forestry paper 171. Rome

Gomez C, Abril S (2012) Nuptial flight of the seed-harvester ant, *Wessor barbarous* (Linnaeus, 1767) (Hymenoptera: Formicidae) in the Iberian Peninsula: synchrony, special scale and weather conditions. Myrmecol News 16:25–29

Hölldobler B (1983) Territorial behavior in the green tree ant (*Oecophylla smaragdina*). Harvard University, Cambridge, Massachusetts, 02138, U.S.A

Kaspari M, Pickering J, Longino JT, Windsor D (2001) The phenology of a Neotropical ant assemblage: evidence for continuous and overlapping reproduction. Behav Ecol Sociobiol 50:382–390

Levin E, Yom-Tov Y, Barnea A (2008) Frequent summer nuptial flights of ants provide a primary food source for bats. Naturwissenschaften 96:477–483. doi:10.1007/s00114-008-0496-3

Offenberg J (2011) *Oecophylla smaragdina* food conversion efficiency: prospects for ant farming. J Appl Entomol 135:575–581

Offenberg J (2015) Ants as tools in sustainable agriculture. J Appl Ecol. doi:10.1111/1365-2664.12496

Offenberg J, Wiwatwitaya D (2009) Weaver ants convert pest insects into food-prospects for the rural poor. In: Proceedings of Tropentag 2009 conference: international research on food security, Natural Resource Management and Rural Development. Hamburg. http://www.tropentag.de/2009/abstracts/full/309.pdf

Offenberg J, Wiwatwitaya D (2010) Sustainable weaver ant (*Oecophylla smaragdina*) farming: harvest yields and effects on worker ant density. Asian Myrmecol 3:55–62

Peeters C, Molet M (2010) Colonial reproduction and life histories. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University, New York, pp 178–195

Peng RK, Christian K (2007) The effect of the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae), on the mango seed weevil, *Sternochetus mangiferae* (Coleoptera: Curculionidae) in mango orchards in the Northern Territory of Australia. Int J Pest Manag 53(1):13–24

Peng RK, Christian K, Gibb K (1998) Locating queen ant nests in the green ant, *Oecophylla smaragdina* (Hymenoptera, Formicidae). Insectes Soc 45:477–480

Peng R, Nielsen MG, Offenberg J, Birkmose D (2013) Utilisation of multiple queens and pupae transplantation to boost early colony growth of weaver ants *Oecophylla smaragdina*. Asian Myrmecol 5:177–184

Rwegasira RG, Mwatawala M, Rwegasira GM, Offenberg J (2014) Occurrence of sexual of African weaver ant (*Oecophylla longinoda* Latreille) (Hymenoptera: Formicidae) under a bimodal rainfall pattern in Eastern Tanzania. Bull Entomol Res. doi:10.1017/S0007485314000868

Rwegasira RG, Mwatawala M, Rwegasira GM, Mogens GN, Offenberg J (2015) Comparing different methods for trapping mated queens of weaver ant (*Oecophylla longinoda*; Hymenoptera: Formicidae). Biocontrol Sci Technol 25(5):503–512. doi:10.1080/09583157.2014.992861

Sribandit W, Wiwatwitaya D, Suksard S, Offenberg J (2008) The importance of Weaver ant (*Oecophylla smaragdina* Fabricius) harvest to a local community in Northern Thailand. Asian Myrmecol 2:129–138

Staab M, Kleineidam CJ (2014) Initiation of swarming behavior and synchronization of mating flights in the leaf-cutting ant *Atta vollenweideri* FOREL, 1893 (Hymenoptera: Formicidae). Myrmecol News 19:93–102

Vanderplank FL (1960) The bionomics and ecology of the red tree ant, *Oecophylla* sp., and its relationship to the coconut bug *Pseudotheraptus wayi* Brown (Coreidae). J Anim Ecol 29:15–33

Way MJ (1954) Studies of the life history and ecology of the ant *Oecophylla longinoda* Latreille. Bull Entomol Res 45:93–112

Way MJ, Khoo KC (1992) Role of ants in pest management. Annu Rev Entomol 37:479–503

Wilson EO (1957) The organization of a nuptial flight of the ant *Pheidole sitarches* wheeler. http://ripley.si.edu/ent/nmnhtypedb/images/pdfs/12459. Accessed 3 Nov 2014