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The Search Rate of the African Weaver Ant in Cashew

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Abstract

Oecophylla longinoda is a species of eusocial colony living ants that prey upon other insects to feed their larva. Many of these insects are considered pests. An ecosystem model of the interactions between an *O. longinoda* colony and its potential prey is under construction by the team behind this article, and it is unknown which functional response equations are useful for eusocial insect colonies. We investigated the search rate of *O. longinoda* using artificial feeding experiments in a Tanzanian cashew *(Anacardium occidentale L.)* orchard to determine the search efficiency of the ants, and to assess which functional response equation can be used for eusocial insects. Artificial feeding experiments consisted of providing each of ten colonies 50 pieces of sardine (175 mg dry weight in average) in cashew trees at time 0 and counting the remaining food items at four intervals of 45 minutes during a seven day period. The equations of Gutierrez-Baumgärtner, Lotka-Volterra, and Nicholson-Bailey were assessed and the Nicholson-Bailey equation was found to be most suitable. The Gutierrez-Baumgärtner equation is useful if the demand for storage can be assessed. A large variation in search rates was found between the observed colonies and this problem is discussed in relation to *Oecophylla* sp. efficacy as a biological control agent.

Introduction

Cashew (*Anacardium occidentale* L.) is the fourth most valuable export crop after coffee, cotton, and tea in Tanzania (Martin et al., 1997). The crop is attacked by a variety of insects that feed on shoots, panicles, and fruits. Among insect pests the mosquito bug (*Helopeltis schoutedeni* Reuter), the leaf-footed bug (*Pseudotheraptus devastans*, Dist.), and the coreid bug *Anoplocnemis curvipes* (F.) are most important (Dwomoh et al., 2009). The damage caused by the bugs reduces the cashew nut quality and yields (Martin et al., 1997), and consequently the farmers' incomes (Peng, 2008).

As most ant species, the canopy dwelling weaver ants, *Oecophylla* sp., require animal protein and honeydew in their diet (Way, 1954a, Lokkers, 1990). They are generalist predators preying upon a great variety of insects, some of which are pest species (Vanderplank, 1960; Way & Khoo, 1992). The weaver ants occur in many fruit orchards in tropic Asia, Australia and Africa where they are important biological control agents in fruit trees, such as mango and cashew (Way & Khoo, 1992; Peng et al., 1999a; Offenberg et al., 2004; Peng & Christian, 2006; Dwomoh et al., 2009)

Dwomoh et al. (2009) showed that *O. longinoda* was as effective in protecting cashew against pest insects as insecticides such as λ-cyhalothrin and cypermethrin + dimethoate. Several studies suggest that with appropriate management weaver ants can significantly increase fruit yield and reduce the use of pesticides (Van Mele, 2008). For instance, research done on Vietnamese citrus showed that farmers who managed *O. smaragdina* in their orchards spent on average half the amount of money on pesticides compared with those who did not (Van Mele & Cuc, 2000). This suggests a significant economic potential of using weaver ants in pest control. In Australia, *O. smaragdina* has been used to control major cashew pests *(*Peng et al., 1999a) with increases in grower revenue by 1500 AUD/year per ha. (Peng et al., 2004). Based on the similarities of the two *Oceophylla sp.*, it is reasonable to believe that *O. longinoda* can provide similar

benefits to cashew producers in Africa. Two *Oecophylla* species are known, *O. longinoda* in Africa and *O. smaragdina* in Asia and Australia and it has been suggested that they can be regarded as one species in many respects (Way, 1954a; Way & Khoo, 1992).

According to Peng et al. (2013), it takes about three years for a weaver ant colony to reach an adequate size to be used successfully in biocontrol. The growth of a colony is affected by the number of founding queens (Peng et al., 2013), augmenting colony size by transplanting pupae from other nests (Peng et al., 2013), by the availability of prey, and by the capacity of the colony to capture the prey. One of the factors affecting the capacity of the colony to acquire prey is the search capacity of the colony. Thus the search rate is a crucial parameter in the understanding of population dynamics of a colony and its capacity as biocontrol agent.

Axelsen, JA et al. (unpublished) developed a physiologically based metabolic pool simulation model (Gutierrez, 1996) to simulate the growth of weaver ant colonies as a function of temperature, prey availability and artificial feeding and this model was the starting point for our field study. In predator–prey models the functional response equation is a core element in simulating the interactions between predator and prey populations, and the search efficiency parameter is an important factor. Information on the functional response and search efficiency of eusocial insects such as *O. longinoda* is crucial in modeling the trophic interactions. The concept of functional response (Holling, 1959) was based on the actions of an individual consumer and may not be applicable to eusocial insects as their behaviour do not only reflect the demand of the single ant, but the demand of the entire colony (Schmid-Hempel et al., 1993) which can be regarded as a super-organism (Hölldobler & Wilson, 2009).

The objective of this study was to investigate the prey search rate of *O. longinoda* colonies in a cashew orchard in Tanzania in order to identify the most appropriate functional response equation to model the food acquisition by *O. longinoda* colonies. This was done by following the removal of experimentally provided small pieces of dried sardines that were used to simulate prey from trees in the cashew orchard, and using these data to estimate the search rate using the three different functional response equations, Gutierrez-Baumgärtner (Gutierrez et al., 1984), Lotka – Volterra (Lotka, 1925; Volterra, 1931), and Nicholson-Bailey (Nicholson & Bailey, 1935).

Methods and Materials

The experiment was carried out in a cashew orchard at the Naliendele Agricultural Research Station, Mtwara, Tanzania (10º21'09.60''S, 40º10'16.24''E). The area is situated on sandy soils and is characterized by an equatorial climate with two rainy seasons each year and an annual rainfall of 900 – 1200 mm. The surrounding area is mainly used for agriculture where cassava is the main crop and cashew is the main cash crop. The cashew trees used in this study were on the average 5.9 m tall (SE = 0.4), had an average crown diameter of 10.9 meters (SE = 0.7), and an average stem circumference of 1.6 meters (SE = 0.1). Most adjacent trees had overlapping branches. Ten mature weaver ant colonies (based on the presence of large worker individuals that are not present in young colonies) were identified and used in the experiment. A weaver ant colony usually consists of many nests scattered in the tree canopy, and a colony may cover more than one tree.

Fifty pieces of bait (simulating a prey item) were placed on a single tree per colony. Prey items consisted of small pieces of dried sardines of approximately equal size, with an average dry mass of 87.5 mg. Five pieces of duct tape were wrapped around 5 different branches in each tree, with the sticky surface pointing outwards. The tape was 1.6 cm wide and its length depended on the thickness of the branch. On each piece of tape we placed 10 pieces of fish, giving a total of 50 pieces of fish per tree. Each piece of tape was placed on the same location in the tree throughout the observation period. The tape was only replaced when needed (when it was wet or when filled with fish scales), so not all pieces of tape were replaced at the same time.

Data collection consisted of counting the number of fish pieces on tapes in each of the 10 trees at intervals of 45 minutes for 3 hours giving data from 4 intervals per day. The experiment was repeated 7 times on different days between 10 am and 2 pm at the beginning of the long rainy season from the 29th of February to the 8th of March 2012.

The background disappearance rate of prey items was investigated on five randomly selected trees kept free of ants. The remaining prey items were counted using the method described above. Other predators beside *O. longinoda* or rain/wind were assumed to have removed the prey.

Calculation of the search rate (*s*) was done by the Gutierrez-Baumgärtner functional response model (Gutierrez, 1996) (1)

$$M^* = D\left(1 - e^{(-sM'/D)}\right) \quad (1)$$

which can be rearranged to

$$s = -\left(\frac{D}{M'}\right)\ln\left(1 - \left(\frac{M^*}{D}\right)\right) \quad (2)$$

where *M'* is the available biomass of prey, *M** is the food collected by predator, *D* is the predator demand for prey (not including sugar), and *s* is the search rate of predator (Gutierrez., 1996). All biomasses were dry weights.

The search rate (*s*) was estimated by equation (2) at fixed time intervals of 45 min., *M'* was controlled (biomass of fish provided), *M** was measured (biomass of fish removed), and *D* was estimated through calculation of the daily colony demand (equation 3):

$$D_{colony} = \Sigma_{all\,castes}\,D_{growth} + D_{reproduction} + D_{Storage} + D_{respiration} \quad (3)$$

D_{growth} depends on the amount of brood present. Brood consists both of larvae and pupae but since pupae do not grow (Hölldobler & Wilson, 1990) and was excluded from this calculation. D_{growth} was calculated according to equation (4).

$$D_{growth} = (N_{ants,t} \times ratio_{l/w} \times m_{larvae}) \times r_g{}^{\Delta t} \quad (4)$$

where $M_{larvae,t}$ was the mass of larvae at the time t, $N_{ants,t}$ was the estimated number of ants in the colony at time t (table 1 and table 3), $Ratio_{l/w}$ was the proportion of larvae compared to workers, m_{larvae} was the average dry weight of larvae, r_g was the maximum growth rate per unit of physiological time, and Δt was the time in physiological time units per day (Taylor, 1971). The expression in the parenthesis of equation 4 calculated the mass of larvae in the colony.

The number of ants was estimated according to Lim (2007) who have presented a non-destructive method to estimate the abundance of *O. smaragdina* within a nest, equation (5):

$$\ln N_{ants} = -1.16 + 1.09 \times \ln V \quad (5)$$

where N_{ants} is the estimated number of ants in a nest, and V is the estimated volume of a nest. Although the equation of Lim (2007) concerned *O. smaragdina*, it was adopted for *O. longinoda* as the two species are very similar in many respects (Way, 1954a; Way & Khoo, 1992).

Number of nests per tree was estimated by dividing each tree into sections, and counting all visible nests from the ground. The numbers of nests in each section of the tree were then added up to give the estimated number of nests in each tree. Only nests built in the surveyed trees were included in the data collection. Many nests were situated high in the tree crowns and it would have been very time consuming to measure their sizes precisely. Therefore, the average volume (V) of nests from the plantation was used. The estimation of average nest volume of the plantation was based on 20 randomly picked nests from the investigated trees. The volume was calculated by assuming the nests to be spherical (Lim 2007) using equation (6) to calculate the volume of the sphere.

$$V = \frac{4}{3}\gamma^3 \quad (6)$$

where γ (= ½ diameter) is the radius of the nest. The diameter was calculated as the average of length, width and height.

$D_{reproduction}$ was expressed only through the reproduction of the queen, as in this species she is the only individual of the colony producing fertilized eggs (Hölldobler & Wilson, 1990). Calculation of this was done by multiplying the total number of ants by the larvae-worker ratio *(ratio_{l/w})*, divided by the developmental time in days. This gave an estimate of the number of new larvae added to the colony from eggs per day, and the input of new larvae were assumed even with the oviposition rate. Multiplying this rate by the dry weight of an egg resulted in the daily demand for reproduction (7):

$$D_{reproduction} = \frac{N_{ants} \times ratio_{l/w}}{T_d} \times m_{egg} \quad (7)$$

where m_{egg} was the average dry weight of an egg and T_d was the development time. $D_{respiration}$ refers to the respiration of the colony, and because ants mainly meet these demands through sugar sources (Caroll & Jansen, 1973; Way, 1954b) and not through protein this parameter was ignored in the calculation of the demand for prey.

$D_{storage}$ refers in the Gutierrez-Baungärtner equation primarily refers to the fat reserve of the predator, but in the case with a colony of eusocial insects it refers to the amount of food being stored within the colony for later use. In calculating the prey search rate according to the Gutierrez-Baumgärtner equation this parameter ignored, as the demand for food to be stored can presently not be quantified.

Results

Several ants (5-10 individuals) were observed carrying single food items together from the tape back to the nest, which demonstrated that the ants were capable of removing the prey items from the tape. Likewise it was observed that two or more ants often worked together in detaching the food items from the tape by forming a bridge.

There was a tendency for higher prey removal (Table 1) at the beginning of the observation period compared to the end but the difference was not significant (Wilcoxon test, DF = 6, p = 0.0895). Colony 1, 2, and 9 showed variable prey-removal rates and had days with very low prey-removal compared to the other colonies. The background disappearance rate was 0.0027g prey per hour (1.46% disappearing per hour).

Table 1. Daily removed prey items in grams (dry weight) per experimental period (180 minutes) in each tree.

Date	Colony 1	Colony 2	Colony 3	Colony 4	Colony 5	Colony 6	Colony 7	Colony 8	Colony 9	Colony 10	Average (SE)
					Grams dry weight						
02.29.2012	2.28	0.96	4.29	3.24	2.80	1.75	1.14	3.68	0.09	2.45	2.27 (0.41)
03.01.2012	0.44	0.61	2.8	2.89	3.85	1.23	1.93	2.71	4.29	4.29	2.50 (0.45)
03.02.2012	0.18	0.44	3.33	3.24	2.36	0.79	1.14	2.71	4.29	3.41	2.19 (0.46)
03.05.2012	0	0.7	2.45	1.84	3.94	1.66	1.31	2.71	0.44	2.8	1.79(0.39)
03.06.2012	0.79	0.26	2.98	2.1	3.68	1.58	0.88	2.71	0.18	3.41	1.86 (0.41)
03.07.2012	0	0	2.71	1.84	3.41	1.66	1.49	0.61	0.09	0.96	1.28(0.37)
03.08.2012	0	0.18	1.49	2.1	2.45	0.35	1.66	0.79	0.18	0.44	0.96 (0.28)
Total	3.69	3.15	20.05	17.25	22.49	9.02	9.55	15.92	9.56	17.76	12.84 (2.14)

The study trees had different numbers of nests, and the estimated ant density per tree varied from about 1900 to about 27000 (Table 2).

Table 2. Estimated number of worker ants in 10 different trees.

Tree nr.	Numbers Nests	Ants per tree
1	11	3592
2	24	7836
3	31	10122
4	18	5877
5	21	6857
6	9	2939
7	20	6530
8	19	6204
9	6	1959
10	82	26774

It was impossible to calculate the search rate in four out of the ten colonies using the rearranged Gutierrez-Baumgärtner equation (2) as the acquired prey exceeded the estimated colony demand. This situation caused the argument of the natural logarithm function in equation 2 to return negative values, which is not defined. This made it clear that the Gutierrez-Baumgärtner equation is not suitable because it is implicitly assumed that the predator does not acquire more than demanded, and hence it is necessary to use a functional response equation that does not rely on colony demand.

As an alternative to using the Gutierrez-Baumgärtner equation in calculating the search rate, a derivation of the Holling's disc equation was tried. Hollings disc equation, like the Gutierrez-Baumgärtner equation, produces a type II functional response that shows the relationship between the number of prey items eaten during a period of time and prey density, leaving out demand (*D*), but including handling time (Holling, 1959). Handling time was in this case ignored as there are so many ants in a colony that the few individuals taking care of prey handling are insignificant and therefore this parameter was ignored. For instance, if 20 ants are handling a prey in a colony housing 1000

large workers there are still 980 to continue searching, making the lack of the 20 ignorable. Leaving out the handling time in Hollings disc equation reduces it to the classical Lotka-Volterra equation giving a simple type I functional response. Thus, based on the Holling's disc equation a new and simple equation (8) to calculate the prey search efficiency was generated

$$M^* = s(\Delta t) \times N \times M' \Leftrightarrow s(\Delta t) = \frac{M^*}{N \times M'} \quad (8)$$

where M^* was food collected by predator per unit time, M' is the available biomass of prey, N was the number of workers in a colony, and s was the search rate of predator during the observation period (45 min).

Another alternative to calculate the search rate was the Nicholson-Bailey equation (Nicholson & Bailey, 1935),

$$M^* = M' \times \left(1 - e^{-s(\Delta t) \times N}\right) \Leftrightarrow s(\Delta t) = -ln\left(1 - \frac{M^*}{M}\right)/N \quad (9)$$

where M^* was food collected by predator per unit time, M' was the available biomass of prey, N is the number of workers in a tree, and $s(\Delta t)$ was the ants' search rate per unit time. This equation is not dependent on the demand rate and assumes that predators are searching randomly and that a group of predators may search overlapping areas.

The search rate for an experimental period (45 minutes) using the Lotka-Volterra equation (8) ranged from 0.01 to 8.29 × 10⁻³ ant⁻¹ and the average *search rate (s)* was 1.29 × 10⁻³ ant⁻¹ (Table 3), which gives an hourly search rate of 1.72 × 10⁻³ h⁻¹ ant⁻¹. The search rate for the same period of time determined by the Nicholson-Baily equation (9) ranged from 0.0 to 8.4 × 10⁻⁵ ant⁻¹, an average search rate *(s)* of 2.3 × 10⁻⁵ ant⁻¹ (Table 4), and an hourly search rate of 3.1 × 10⁻⁵ ant⁻¹. The lower removal of prey items during the last two days was not reflected in a significantly lower search rate (Wilcoxon, df = 6, p = 0.597 and p = 0.209 calculating s according to the Lotka-Volterra and Nicholson Bailey equations, respectively) but a paired t-test between the first and the last date revealed a significant difference using s-values calculated using the Nicholsom-Bailey eqution, indicating an effect of date which may have been obscured in the Wilcoxon test by the large variance. Furthermore, there was a highly significant difference in search rate between the weaver ants in the investigated trees (Wilcoxon, df = 9, p < 0.0001) using s-values from both equation.

Table 3. The estimated search rates (×10⁻³) per observation period (45 min) for each colony on each day using the Lotka-Volterra functional response equation.

Colony	1	2	3	4	5	6	7	8	9	10	Average (SE)
02/29	0.48	0.46	4.56	1.80	1.20	0.35	0.47	2.02	0.01	5.45	1.68 (0.59)
03/01	0.09	0.28	2.26	1.60	2.31	0.23	0.83	1.30	0.05	5.90	1.49 (0.56)
03/02	0.04	0.20	2.96	1.92	1.02	0.14	0.47	1.27	0.48	8.27	1.68 (0.79)
03/05	0.00	0.33	1.84	0.86	2.43	0.33	0.55	1.33	0.05	5.90	1.36 (0.56)
03/06	0.17	0.12	2.41	0.99	2.08	0.29	0.35	1.26	0.02	8.29	1.60 (0.79)
03/07	0.00	0.00	2.01	0.86	1.82	0.33	0.64	0.23	0.01	1.61	0.75 (0.25)
03/08	0.00	0.08	0.99	1.01	1.08	0.06	0.73	0.30	0.02	0.69	0.50 (0.14)
Average (SE)	0.11 (0.07)	0.21 (0.06)	2.43 (0.42)	1.29 (0.17)	1.71 (0.22)	0.25 (0.04)	0.58 (0.06)	1.10 (0.24)	0.09 (0.07)	5.16 (1.12)	1.29

Table 4. The estimated search rates ($\times 10^{-5}$) per observation period (45 min) for each colony on each day using the Nicholson-Baily functional response equation.

Colony	Search rates (Nicholson-Baily equation)										
	1	2	3	4	5	6	7	8	9	10	Avg. (SE)
02/29	5.0	0.8	6.2	5.7	3.7	4.3	1.2	7.4	0.3	0.9	3.5 (0.7)
03/01	0.7	0.5	2.5	4.6	7.7	2.8	2.2	3.9	1.3	1.0	2.7 (0.4)
03/02	0.3	0.3	3.5	5.7	2.8	1.7	1.2	3.9	1.3	1.4	2.2 (0.3)
03/05	0.0	0.6	2.0	2.3	8.4	4.1	1.4	3.9	1.3	1.0	2.5 (0.5)
03/06	1.4	0.2	2.8	2.8	6.7	3.8	0.9	3.9	0.5	1.4	2.4 (0.4)
03/07	0.0	0.0	2.4	2.3	5.5	4.1	1.6	0.6	0.3	0.2	1.7 (0.3)
03/08	0.0	0.1	1.0	2.8	3.0	0.7	1.8	0.8	0.5	0.1	1.1 (0.2)
Avg. (SE)	1.1 (0.6)	0.4 (0.1)	2.9 (0.6)	3.7 (0.5)	5.4 (0.8)	3.1 (0.5)	1.5 (0.2)	3.5 (0.8)	0.8 (0.2)	0.8 (0.2)	2.3 (0.1)

Discussion

In this paper we present the first attempt to estimate the prey search efficiency of a eusociale insect species. Additionally, we present the choice of a functional response equation useful for eusociale insects, which has not been attempted before. The Gutierrez-Baumgärtner equation generally works well with solitary living insects (Gutierrez, 1996)*,* where the demand is a readily quantifiable parameter. In this case the equation could not be used, as *O. longinoda* is a eusocial colony living insect, were colony demand is difficult to quantify, as the maximum demand for storage seems to be virtually unknown. The storage may be very large as ants are known to carry prey items too large to be consumed immediately to their nests (Hölldobler & Wilson, 2009), and are capable of concealing large prey items by covering them with leaves (Rastogi, 2000). Additionally the workers can collect and store food for a short period in their crop, but eventually they digest it (Eisner, I957; Eisner & Brown, I958). Workers are also capable of laying trophic eggs serving as a food reserve that can be eaten in times of need (Carbaugh & Judd, 2011). However, we do not know how much food they conserve in these manners, and a quantification of $D_{storage}$ will be very difficult with known methods, and therefore the search rate for these eusocial colony living insects can presently not be calculated by the Gutierrez-Baumgärtner functional response equation.

As long as the colony demand is unknown it is necessary to use a functional response equation that does not rely on estimates of the colony demand for storage, and the Nicholson –Baily equation (equation 9) is a good possibility. The Nicholson-Baily functional response equation assumes that the population of predators searches their habitat randomly and that they do not affect each other, which may cause their searched areas to overlap. Ants are known to communicate on attracting other colony members to larger preys (Hölldobler, 1983; Wojtusiak et al., 1995; Deneubourg

et al., 2002) causing an aggregated response to larger prey items (Crawley, 1992), and in that case the two assumptions fail. However, this aggregated response only seems to apply to larger prey items that cannot be carried by one or a few ants, and does therefore not apply to our situation where single or a few ants were observed to carry the food items. Most *O. longinoda* prey items are smaller insects that can be carried by single ants (Lynegaard et al., 2014). On the other hand, situations where the ants generally feed on larger food items such as larger beetles, cockroaches, dragon flies, larger moths, butterflies, lizards or dead mammals may occur, and in such cases aggregated responses can be expected and the assumptions behind the Nicholson-Bailey equation fail. In these cases, the only useful functional response equation is the Lotka-Volterra equation (equation 8). The acceptance of both equation (8) and (9), which are linear models, as useful to calculate the prey search rate, is supported by (Fast et al, 2015) whose results suggest *O. longinoda* to follow a functional response type I (a linear response), as it was not possible to safely identify a saturation point of the functional response curve.

The value of the average search rate cannot be compared with the results from other investigations, as we have found no similar attempts to estimate this parameter for eusocial insects in the literature. Instead, it should be possible to compare with estimates of search rates from solitary insects, but this is problematic because estimated search rates depend to a large extend on the experimental arena and may come out in different units (*e.g.* De Kranker et al., 2001*;* Madadi et al., 2011; Sentis et al., 2012; Mrosso et al., 2013). No or at least very few investigations have been dealing with estimating the search rate under field conditions. Therefore, the outcomes presented here are valuable as they were obtained under field conditions and, furthermore, on a eusocial insect species.

There is a long list of papers on *O. smaragdina* and *O. longinoda* used in pest control (see review of Van Mele, 2008; Offenberg, 2015) but there is virtually no knowledge on

factors that control their efficacy, except ant density (Peng et al., 2013) and boarder fights (Peng et al, 1999b). Knowledge on other factors affecting efficacy as for instance the highly variable search rates between colonies found in this paper suggests that there are some important factors controlling the predatory behavior of a weaver ant colony. These factors may for instance include the amount of available sugar, which is crucial as fuel for ant colonies (Holldöbler & Wilson, 1990), and the colony search effort for insect prey may depend on the colony´s access to sugar. Sugar sources are usually honeydew excreted from hemipterans (aphids, scale insects, mealy bugs, etc.), floral nectaries, and extra-floral nectaries as found on newly produced leaves, inflorescences and young nuts of cashew (Peng et al., in prep). Therefore, the satiation of a weaver ant colony with sugar must depend on the presence of these sources, which in the case of floral nectar will depend on flowering, and the production of extra-floral nectar in cashew will depend on the flushing period when trees produce new leaves and inflorescences. Populations of hemipterans may also vary over the season and between trees. Therefore, access to sugar is very likely to show seasonal fluctuations as well as differences between colonies. Also the amount of growing larvae in the colony may affect the demand for protein and in turn the prey search effort. If there is little brood in the colony there is less reason to gather prey as the larvae are the primary consumers of protein in ant colonies (Sanders et al., 1992).

It is of great importance for the possibilities of modeling weaver ant efficiency as biocontrol agents to have good estimates of the search rate and to know which factors are controlling it, as the search rate is essential in the modeling of predator – prey relationships. With the knowledge presented in this paper, modelers now have a figure of the search rate to use in model parameterization. The results presented here have, however, raised some new questions on the possible seasonal variability in search rate, but our results are a first step towards a better understanding of the predation efficiency of weaver ant colonies.

A yet unpublished model (Axelsen JA, unpublished) has been constructed to simulate the colony development of weaver ants (Oecophylla sp.) depending on available amounts of sugar and protein. As there is no information available to simulate the amount of available sugar from natural sources in cashew trees the modeled daily amount of available sugar in the model can be regarded sugar feed to the colony by cashew growers. Similarly, the model has been constructed to simulate what feeding the colony with meat as a protein source means to the colony growth. By simulating the colony growth based on manipulations of sugar and protein sources by the cashew grower it becomes possible to simulate how quickly a colony can be brought to a size large enough for effective biocontrol. According to Peng et al. (2004) it takes at least two years for a colony to grow to an efficient size, but supplementing with artificial feeding this is likely to be achievable much faster. The link between the colony size

and its functioning in biocontrol is the search rate, and the figure on the search rate from this paper makes it possible to simulate how much prey is captured in a cashew tree at a given prey density. This prey may include pest species, and therefore, the results on the search rate presented here are very important for linking colony size to biological pest control in cashew plantations.

Acknowledgements

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