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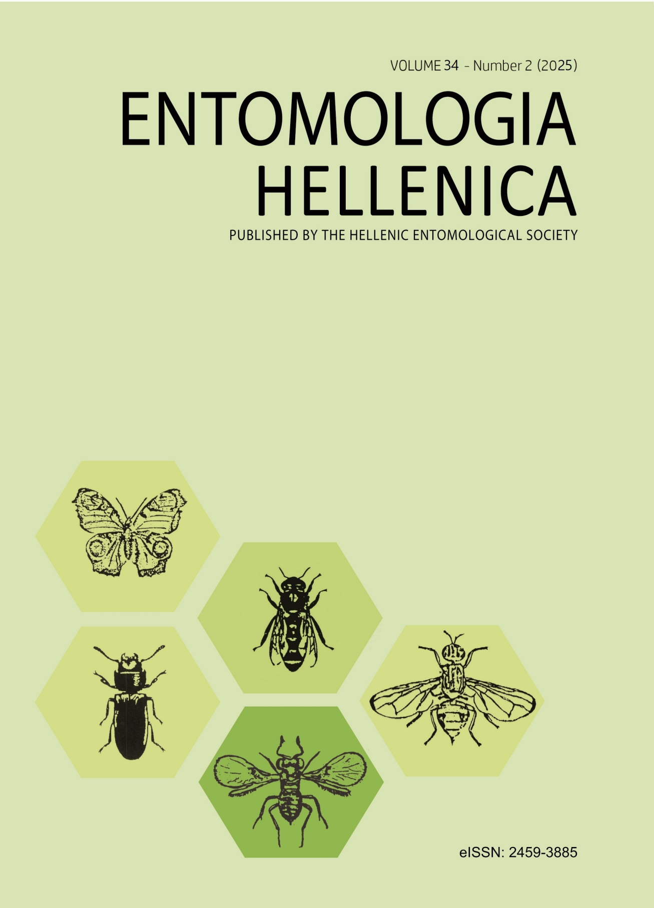

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Khokan Naskar, Dr. Srimanta Kumar Raut, Dr. Sangita Maiti Dutta

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Precautious cooperative food transportation behaviour in the weaver ant *Oecophylla smaragdina* (Fabricius): weaver ant's secret to efficient food delivery

KHOKAN NASKAR[1, 3], SRIMANTA KUMAR RAUT[2], SANGITA MAITI DUTTA*[3]

[1]*Department of Zoology, Achhruram Memorial College, Jhalda, Purulia-723202, West Bengal, India*

[2]*Ecology and Ethology Laboratory, Department of Zoology, University of Calcutta, 35, Ballygunge Circular Road, Kolkata - 700019, India*

[3]*Biodiversity and Environmental Studies Research Centre, Department of Biological Sciences, Midnapore City College, Kuturia, P.O. Bhadutala, Paschim Medinipur - 721129, West Bengal, India*

ABSTRACT

The weaver ants, *Oecophylla smaragdina* (Fabricius), are arboreal in habit. They typically collect prey animals either from different parts of the nest tree or from the ground around it. In the present study we observed the food-transporting behaviour of these ants in Jhalda, India (Latitude-23º22′ North and Longitude 85º59′ East), specifically focusing on those foraging on the ground. We found that, depending on the size/weight of the prey, the ants have developed a process of cooperative food transportation vertically on the tree trunk. The transport of prey, especially *Camponotus compressus* (Fabricius) ants, is affected by the required number of transporters acting as pullers and pushers, depending on the prey's size/weight. Simultaneously, a corresponding number of workers can be seen following the food-carrying group all along until the food is lodged into the nest. The differences in the number of workers involved in vertical food transportation are statistically significant, as are revealed by the results of a one-way ANOVA test and Tukey's HSD test ($P < 0.05$).

KEY WORDS: *Cooperative prey transportation, helper transporters, predation, prey animal size/weight, vertical surface*.

Introduction

Weaver ants, *Oecophylla smaragdina* (Fabricius), are found in tropical Asia and Australia. They play an important role in the ecosystem of tree canopies in humid tropical regions (Blüthgen and Fiedler, 2002). Workers of this species construct the nests in the trees by weaving leaves together using larval silk (Majno, 1991).

O. smaragdina feed on insects and various invertebrates, typically preying on beetles, flies, and hymenopterans while vertebrates like lizards, mice and birds are not excluded from their diet (Kusters and Belcher, 2004, Burchill et al., 2022). Since these ants build their nests in the canopy of tall trees (Kusters and Belcher, 2004, Braby, 2004) they are also met close to aphids, scale insects and other homopterans

**Corresponding author: smaitiduttazoo@gmail.com*

to feed on honeydew, they produce, primarily in canopies linked by lianas (Blüthgen and Fiedler, 2002). However, *O. smaragdina* primarily relies on prey animals for its nutrition. Consequently, the species has developed cooperative food transportation behaviour to carry unmanageably large prey items from either the branches of the host tree or the ground foraging area surrounding the tree. This transportation behaviour involves both horizontal and vertical movement of worker ants in a group, ensuring the procurement of food items of various weights, sizes and shapes to the nest regardless of their source.

Cooperative food transportation in ants has drawn significant research attention (McCreery and Breed 2014, Naskar and Raut, 2015a, b, Buffin and Pratt, 2016, McCreery, 2017, Feinerman et al., 2018, Ron et al., 2018, Hisamato et al., 2020, Burchill et al., 2023). The genesis of such transportation has also been discussed by Naskar and Raut (2019). The proximate mechanisms in connection with cooperative transportation in ants have also been discussed at length by McCreery and Breed (2014) in their review. Moreover, Czaczkes and Ratnieks (2013) have provided a thorough description of the cooperative transport mechanisms in ants and other animals.

Qin et al. (2019) described how the imported fire ant, *Solenopsis invicta* (Buren), transports food vertically while Burchill et al. (2023) extensively discussed the rate of prey delivery during collective vertical transport of *O. smaragdina*. However, the coordinating mechanisms that enable this behaviour remain under investigation. In our studies of the environmental cues and trailing behaviour of *O. smaragdina*, in Jhalda, India (Latitude- 23º22′ N Longitude - 85º59′ E), we had the opportunity to study the cooperative food transporting behaviour of certain prey items, where the workers exhibited their behaviour for specific prey items. The workers exhibited behaviours such as positioning themselves around the prey in direct contact as needed to carry the prey, while some workers were seen crawling following the transporters as they moved upward on the tree trunk to transport the prey into the nest.

We hypothesized that *O. smaragdina* ants need a 'helper group' to ensure vertical transportation of the prey, to transport the same into the nest located in the canopy region of the tree.

We hypothesized that the weaver ants *O. smaragdina* have developed a strategy to exhibit increased caution when transporting prey on vertical surfaces. This involves recruiting additional workers beyond those directly involved in carrying prey. We propose that this cooperative transportation system helps overcome obstacles and prevents prey from falling.

To test this hypothesis, following our observations on the capturing behaviour (Naskar et al., 2025), we experimentally offered prey-ants (*C. compressus*) of varying lengths and weights to *O. smaragdina*, in their natural foraging ground. The results of this experiment demonstrate a clear correlation between prey size and the number of helper workers involved in vertical transport.

Materials and Methods

Insect: The orange weaver ants, *O. smaragdina*, constructed their nests in a large mango tree, *Mangifera indica* (Linnaeus), located on the campus of Achhruram Memorial College, Jhalda, Purulia, West Bengal, India. These ants are locally known as Kurki and are even consumed as food by locals (Mitra et al., 2020). We focused on this particular mango tree. The nests were located high up on the tree, between 8 and 14 meters above ground. Freshly killed *C. compressus* individuals were offered as prey to *O.*

smaragdina weaver ants, at different times during morning hours, between March to June 2024. *C. compressus* belonged to three different size and weight groups, viz. Group A (length 1.6-1.8 cm, mean 1.66 ± 0.02 Standard Error (SE) cm, and weight 19-22 mg, mean 20.84 ± 0.32 SE mg), Group B (length 1.0-1.3 cm, mean 1.15 ± 0.03 SE cm, and weight 6.5-7.4 mg, mean 6.81 ± 0.08 SE mg), and Group C (length 0.6-0.8 cm, mean 0.72 ± 0.02 SE cm, and weight 4-8 mg, mean 5.8 ± 0.41 SE mg) (Fig. 1). Three prey individuals were offered, taking only one from each group in each trial.

We observed the number of *O. smaragdina* individuals engaged in transporting offered *C. compressus* prey individuals, as well as the number of workers following the transporter group.

Live *C. compressus* were collected from the foraging ground surrounding a nest-building mango tree on the Achhruram Memorial College campus in Jhalda, Purulia, West Bengal, India. Three individuals from each size group were killed, measured, placed near the tree base, and observed between 08:00 h and 09:00 h from March to June 2024. Observations continued until one individual was captured by *O. smaragdina* predators within the said specified time period of one hour.

This process was repeated for a total of 48 trials (14 in March, 15 in April, 11 in May, 8 in June). Of these, in 6 of the trials predation activity was not exhibited by the predators during the specified time period, so these trials were discarded. In the remaining 42 trials, data was collected successfully. Considered data included the number of *O. smaragdina* directly involved in prey transport and the number of follower workers, considering 10 events with respect to 10 predator individuals of each size group. Thus, the remaining 12 predation events were rejected.

It is to be mentioned here that we had the opportunity to follow the movement of *O. smaragdina* all the way up to the nests, which were located between 8-10 m height above ground.

Statistical analysis: We applied a one-way analysis of variance (ANOVA) to determine whether the number of worker weaver ants that followed the groups carrying large (Group A), medium (Group B) or small (Group C) *C. compressus* prey items was statistically significant. If the ANOVA result was significant, we performed Tukey's HSD (Honestly Significant Difference) test to verify whether the difference between two means in respect to the number of *O. smaragdina* workers following the food-carrying groups were significant at a significance level of $\alpha > 0.05$.

Results and Discussion

The results of the present study are depicted in Figure 1. It is a well-established fact that most ant species construct their nests in the ground. They usually collect food from the foraging ground, mostly individually but occasionally cooperatively. The cooperative transportation strategy is developed simply to carry a large prey item, which is indispensable for the colony members, but unmanageable for one single transporter to carry it into the nest. Since most ant species collect their food from the foraging area confined to the ground, it is easy to transport the prey item cooperatively on a horizontal surface (Wojtusiak et al., 1995, Yamamoto et al., 2009). In contrast, some ground-dwelling ant species collect their food from high trees, while others have adapted to lead an arboreal life and procure their food from the ground, individually or cooperatively (Traniello and Beshers, 1991, Robson and Traniello, 1998, Yamamoto et al., 2009, Czaczkes and Ratnieks, 2013, Buffin and Pratt, 2016). Also, some ant species are well adapted to carry their food cooperatively from the floor of a house to the roof horizontally. However, it is believed that the strategy developed by each ant species varies considerably depending on the skill of the transporters to manage the transported prey item. For this reason, a significant number of species has developed the art of cutting large-sized prey into small pieces to enable the transporter to transport a piece of prey individually or cooperatively by a small group of ants.

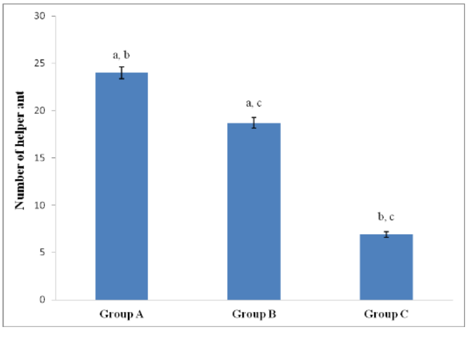

FIG. 1: Number of helper ants *Oecophylla smaragdina* involved in the vertical transportation of a *C. compressus* belonging to Group A, B or C, on the trunk of the nesting tree (a, b and c indicate significant differences among means).

Irrespective of horizontal or vertical transportation, the ants need the cooperation of some workers other than the number of individuals who are engaged in transportation. This happens because some transporters become tired during long-distance transportation, and other workers must replace them, simply to ensure transportation of the prey item to the nest. Moreover, on the horizontal surface, the transporter group, when failing to cross a hurdle, needs the assistance of more workers, either as pullers or as pushers. Likewise, vertical transportation also depends on the interim assistance of some workers, either to give relief to the tired ones, to cross hurdles, to help in pushing and holding the prey in cases steepness is high, or when the prey must be carried hanging downwards. Therefore, the presence of extra workers near the transporter group is a prerequisite for successful transportation. Horizontal transport is simpler because the prey can be dropped on the ground for a while to allow recovering and restarting after the rest or to get some workers wandering in the foraging ground, in touch, to overcome the problem of transportation (Naskar and Raut, 2018). Also, *Formica japonica* (Motschoulsky) exhibited behavioural diversity assisting obstacle navigation during cooperative transportation (Utsumomiya and Takamatsu, 2017). Yet, these strategies are not applicable for vertical transporters. If these release the prey from their grip, the prey will drop down. So, ant species adapted to carry the prey vertically would be firstly extremely cautious to hold it, then ensure transportation. This is why *O. smaragdina* has developed the strategy of forming a 'helper group' (Fig. 2) to continually follow the food carrying group. It is also to be mentioned here that, *O. smaragdina* ants use a clever strategy as they are able to anticipate how many helper workers are needed to follow the food carrying group. Surely, such a decision is very much influenced by the number of workers actually needed to carry the prey item and the distance to be covered to reach the nest.

FIG. 2: Food carrying behaviour of *Oecophylla smaragdina* on a vertical tree surface. Note the transporters involved in transportation cooperatively and the helper group following the transporter group.

Food transportation behaviour in the arboreal ants *Crematogaster clariventris* (Mayr), *Tetraporium acculeatum* (Mayr), *Oecophylla longinoda* (Latreille), *Platythyrea conrradti* (Emery) and *Myrmicaria opaciventris* (Emery) has been documented by Zephirin et al. (2021). But, among all arboreal ant species, *Gnamptogenys menadensis* (Mayr) and *Oecophylla smaragdina* (Fabricius) are the only exceptional species that retrieve unusually large prey items in cooperative ways. These two species, particularly *O. smaragdina* (Fabricius) and *O. longinoda* (Latreille) have remarkably developed tarsi that allow them to grip plant surfaces effectively (Freeland et al., 1982, Wojtusiak et al., 1995, Federle et al., 2001). This likely contributes to their strong grip and successful cooperative prey retrieval in their arboreal habitat (Wojtusiak et al., 1995, Federle et al., 2001). Interestingly, while both, *O. smaragdina* and *O. longinoda* are arboreal, they descend to collect prey from the ground. In contrast, *G. menadensis* is strictly arboreal, never leaving the trees and relying on food available on its host (Gobin et al., 1998).

Notably, *O. smaragdina* appears to be a step ahead of other arboreal ants in an effective strategy for transporting prey on vertical surfaces, specifically straight tree trunks. To prevent the prey from falling, they utilize a helper group that follows the food-carrying group. This species also shows a remarkable ability to tailor the size of the helper group based on the prey size or weight and the distance to the nest. As observed, the helper group size varied from 21-26, 16-22, and 5-8 individuals, depending on the carrier group size of 10-12, 7-8, and 2-3 workers, respectively. Evidently, this behavioural adaptation for vertical transport is highly influenced by the prey's size or weight and the distance to be covered.

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