

Ants' cooperative food retrieval: A review

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Abstract

Ants' food retrieval behaviour has drawn the attention of various workers. It is now well established that ants forage at large, individually here and there in their foraging area. An individual forager when comes across a food item which is self-manageable to carry the same to the nest then she finds no problem to procure the same to the nest. But, if the food item is heavy and unmanageable for her to procure the same to the nest then she looks for the arrival of the nest-mates. Depending upon the available food source they apply trail pheromone along their pathway to and fro from food source to the nest. They apply different food carrying strategies, depending upon the nature of food, that is, either liquid or solid. Following decision the nest mates retrieve the targeted food item either individually or cooperatively as such, and/or cut the same into pieces to ensure procurement of these fragments either individually or in small groups. But, earlier reviewers though have paid due attention on the decision making processes and cooperative food transportation no analysis have been done in respect to fragmentation of food item and retrieval behaviour of the same. Also no attention has ever been paid to analyze the retrieval mechanism of liquid and semi liquid foods. Thus, this review presents a holistic approach of ants' food retrieval mechanisms highlighting the possible trends of development of the process.

Keywords: Ants' foraging area, food item, transportation behaviour

Introduction

A lot of attempts have been made to get a comprehensive idea on different aspects of ant species occurring throughout the globe (Guenard *et al.* 2017) [19]. According to Gibb and 72 co-workers (2017) [17], in respect to abundance of 51,388 types of ants based on global database, more than 2,693 species and 7,953 morphospecies have been recorded depending on the collection at 4212 locations around the world. However, as per updated edition of Wikipedia (January 2022) it is evident that more than 13,800 of an estimated total of 22,000 species have been classified. In contrast, earlier, on 3rd July 2018 in Myrmecological News Blog, Florian M. Steiner and others stated 13,379 valid extant ant species and around 30,000 are yet to be discovered.

Of the recorded ant species a very limited number of species belonging to different genera have been paid due attention to study their biology, ecology and economics. It is evident that the ants feed on nectar, seeds, fungi, plant-saps, and various types of animals as prey as well as on dead and decomposed animals (Sudd 1960 [44]; Wilson 1963 [49]; Sudd and Franks 1987 [45]; Fischer *et al.* 2003 [12]; Sengupta *et al.* 2010 [43], Nyaukondiwa and Addison 2014) [36]. Even, ants are adapted to live absolutely on liquid food (Paul and Rocas 2003) [37].

Reports on the foraging behaviour and food transporting strategies have been described by a good number of workers in different ant species. It is an established fact that the ants have developed the art of searching food from different sources in their foraging area and to carry the food materials either individually or cooperatively depending upon the shape and size/weight of the targeted food items to be taken to the nest. In the present article an attempt has been made to review the food retrieval mechanisms in various ant species with a view to assess the evolved behaviours of food transportation and the genesis of the evolved behaviours in respect to the nature of food item and the type of ant species involved.

A prelude of ants' food retrieval mechanism

Ant's foraging area varies to a great extent in respect to species and the type of food they need. Available reports indicate that the ants thrive both on liquid and solid foods. Liquid foods may be nectar, body fluids of certain animals (caterpillars, termites etc) and fat. On the other hand they feed on various types of solid foods like seeds, fruits, grains, flesh etc. Therefore the food retrieval device varied primarily on the basis of the nature of food i.e. liquid or solid. Again, the devices exhibited by the ants to retrieve the solid food items are accomplished by different means, i.e. either singly or cooperatively (Table 1).

Table 1: Food retrieval devices exhibited by different ant species.

| Ant species | Food transporting device | Author |
|------------------------------|---|-------------------------------------|
| <i>Oecophylla longinoda</i> | Snakes, birds and bats are carried collectively even vertically up the tree trunk. Though variations in cooperative transport are well marked in most cases the workers enabled them to carry the food item effectively to the proper site. | Wojtusiak <i>et al.</i> (1995) [50] |
| <i>Oecophylla smaragdina</i> | Workers carry the young larvae and pupae of silkworm <i>Antheraea mylitta</i> cooperatively to their nest. | Gathalkar (2014) [15] |
| <i>Monomorium destructor</i> | Workers cut the prey into small pieces and the fragmented parts are transported to | Gathalkar and Sen (2018) [16] |

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| | the nest either singly or in groups. Also the manageable prey is transported as such to the nest cooperatively. | |
| <i>Monomorium minutum</i> | Cooperatively transported the silkworm larva to the nest. | Gathalkar and Sen (2018) [16] |
| <i>Polyrhachis bicolor</i> | Workers drag the spinning larvae of tassar silkworm in a group to lodge the same into their nest. | Gathalkar and Sen (2018) [16] |
| <i>Myrmecaria brunnea</i> | Workers are habituated to carry the larvae and pupae of silkworm in groups. | Gathalkar and Sen (2018) [16] |
| <i>Pheidologeton diversus</i> | Transported tassar silkworm larvae and pupae in groups. | Gathalkar and Sen (2018) [16] |
| <i>Tapinoma melanocephalum</i> | Attacked the larvae and pupae of tassar silkworm in groups and also carry the same in groups to the nest. | Gathalkar and Sen (2018) [16] |
| <i>Tetraponera rufonigra</i> | Transportation of food item, the larvae and/or pupae of tassar silkworm in groups is a common phenomenon. | Gathalkar and Sen (2018) [16] |
| <i>Camponotus compressus</i> | Capture and carry the larvae and pupae of tassar silkworm in groups. | Gathalkar and Sen (2018) [16] |
| <i>Paratrechina longicornis</i> | When single individual fails to move the food item alone emits a recruitment signal that recruits nearby nest mates to carry the food item cooperatively to the nest. | Czaczkes <i>et al.</i> (2011) [9] |
| | Cooperatively carry large food items to the nest. | Ron <i>et al.</i> (2018), [41] McCreery <i>et al.</i> (2019) [27] |
| <i>Pheidole roberti</i> , <i>Paratrechina longicornis</i> | Transport food individually or cooperatively depending upon the weight, size and shape of the food. Cooperative transportation is an induced impact of the food's characteristics features. | Naskar and Raut (2018) [35] |
| <i>Novomessor cockerelli</i> | Workers evolved impressive skills of cooperative transport of the food item. | Buffin and Pratt (2016) [3] |
| <i>Eciton burchelli</i> | Transport the food item in a team. The workers have developed the art to carry more weight together than the summed efforts of each ant working alone. | Franks <i>et al.</i> (1999, 2001) [13] |
| <i>Dorylus wilverthi</i> | Workers exhibit almost similar cooperative food transporting behaviour like those of <i>Eciton burchelli</i> workers. | Franks <i>et al.</i> (1999, 2001) [13] |
| <i>Pheidole crassinoda</i> | Large sized prey is transported cooperatively to the nest. | Sudd (1960) [44] |
| <i>Pheidole pallidula</i> | Depending upon the size and weight of the food item workers decide to transport the same to the nest collectively. | Toffin (2003) [46] |
| <i>Leptothorax albipennis</i> | Workers are apt to take decision to carry a specific food item, when needed, collectively. | Pratt <i>et al.</i> (2002) [38] |
| <i>Solenopsis invicta</i> | Food size of two into 2x2 mm or more (meat) required cooperative transporting by the workers sometimes, without coordination among the workers. | Wang <i>et al.</i> (2016) [48] |
| | Food item is carried cooperatively when possible, but in cases of unmanageable food item the workers cut the same into pieces and then the fragmented parts were either carried individually or collectively to the nest. | Qin <i>et al.</i> (2019) [39] |
| <i>Pheidole oxyops</i> | Cooperative transportation is pronounced. During transportation they try to avoid dragging. | Czaczkes <i>et al.</i> (2011) [9] |
| <i>Pheidole roberti</i> | Carry the food items individually or collectively to the nest. Transportation of a mosquito is effected only through cooperative transportation. | Naskar and Raut (2014a) [31] |
| | The ants carry the sugar cubes to the nest either individually or cooperatively. | Naskar and Raut (2014b) [32] |
| | Food retrieval procedure was effected by lifting, pulling, pushing. | Naskar and Raut (2015a) [33] |
| <i>Cataglyphys floricola</i> | Cooperative food transport is effective when the food item is located with a distance of 1 m from the nest. | Amor <i>et al.</i> (2009) [11] |
| <i>Aphaenogaster senilis</i> | Workers take part as puller or pusher at respective positions of the food item to be carried cooperatively to the nest. | Cérda <i>et al.</i> (2009) [5] |
| <i>Gnamptogenys moelleri</i> | Depending upon the size of the food item workers are recruited to carry the food cooperatively to the nest. | Cogni and Oliveira (2004) [6] |
| <i>Formica inscirta (=schaufussi)</i> | Group retrieval maximizes foraging efficiency. Coordination of cooperative transportation depends on the "scout" who originally found the food. Irrespective of the size the workers participate in the group. | Traniello (1987) [47] |
| <i>Iridomyrmex purpureus</i> | Depending upon the size and weight of the food item workers decide to procure the same collectively. | Briese and Macaulay (1981) [2] |
| <i>Iridomyrmex darwiniensis</i> | Workers may carry the food item cooperatively as such or after cutting the same into small pieces. | Briese and Macaulay (1981) [2] |
| <i>Pheidologeton diversus</i> | Workers transported earthworms and certain insect larvae as such by large groups. | Moffett (1987) [29] |
| <i>Pheidologeton silens</i> | Workers are habituated to chop the large food item into small pieces and then these pieces are carried either individually or collectively. | Moffett (1988) [30] |
| <i>Pachycondyla laevigata</i> , <i>P. commutate</i> <i>P.(termitopone) marginata</i> | Following group predated the workers carry the prey cooperatively to the nest. | Hölldobler <i>et al.</i> (1996) [22] |
| <i>Lasius neoniger</i> | Transport group size is correlated with prey weight but the size of the workers involved in the retrieval process has little impact. | Traniello (1987) [47] |
| <i>Myrmica americana</i> | Cooperative food transport is effected by the active participation of workers irrespective sizes. | Traniello (1987) [47] |
| <i>Monomorium minimum</i> | Workers of all sizes take part in transportation of food item into the nest. | Traniello (1987) [47] |
| <i>Monomorium pharaonis</i> | They evolved both individual and group food carrying strategies, tearing the food into small fragments individually or pulling and pushing in a group. | Naskar and Raut (2015b) [34] |
| <i>Leptanilla japonica</i> | The workers paralyze the prey in a group and then begin to drag the same towards the broad pile jointly. | Masuko (1990) [25] |
| <i>Oligomyrmex overbecki</i> | The whole dead fruit flies near the nest entrances were sometimes dragged into the nest by groups of 2-5 workers. However, group transport behaviour is poorly coordinated. | Moffett (1986) [28] |
| <i>Camponotus pennsylvanicus</i> | Carry the liquid food and regurgitate the same into the mouth of ants living inside | Hamilton <i>et al.</i> (2010) [20] |

| | the nest. | |
|---|---|---|
| <i>Cataglyphis iberica</i> | Store the liquid food in the crop and regurgitate the same into the mouth of colony members inside the nest. | Dahbi <i>et al</i> (1999) ^[11] |
| <i>Diacamma cf. indicum</i> | Workers carry a drop of liquid between the mandibles through surface tension and share the same with nest mates. | Fujioka <i>et al</i> (2022) ^[14] |
| <i>Camponotus inflatus</i> | Carry the sugary fluid and nectar storing them inside the crop and released the same into the mouth of honey pot ant “repletes” inside the nest. | Conway (1991) ^[8] |
| <i>Ectatomma tuberculatum</i> , <i>Creamatogaster limata</i> | Collect liquid food and stored inside the crop; and transported the same to the nest to distribute the same to the nest mates through a behavior called trophallaxis. | Richard <i>et al</i> (2004) ^[40] |
| <i>Myrmecocystus mimicus</i> | Collect and carry sap and nectar from flowers and honeydew from aphids. Store these liquids in their crop and transfer the same to honey pot ant in the nest. | Hölldobler (1981) ^[21] |
| <i>Melophorus bagoti</i> | Feed on sugary plant exudates and are adapted to carry the same in the crop to store in the abdomen of specialized workers, the so called repletes or “honey pots” | Schultheiss <i>et al</i> (2010) ^[43] |

Retrieval devices for liquid food

During foraging, workers belonged to the genera *Camponotus*, *Cataglyphis*, *Leptomyrmex*, *Melophorus*, *Myrmecocystus*, *Plagiolepis*, *Prenolepis*, *Carebara*, *Diacamma* and *Cephalotes* (Conway 1986^[7], 1991^[8], Paul and Roces 2003^[37], Schultheiss *et al* 2010^[42], Gordon, 2012^[18], Khalife and Peeters 2021^[24], Fujioka *et al.* 2022^[14], Islam *et al.* 2022^[23]) collect fluids which are stored in the upper part of their digestive system (the crop). At nest these workers regurgitate a portion of their stored fluid and pass the same on to other nest mates. On the contrary some ants are used as living food storage vessels in an ant colony. In such colony larger bodied ants called “majors” are accustomed to store nectar, water, fat/ or some other type of liquid foods (such as body fluids of caterpillars and termites) to supply the same to the colony members in future as per requirement. Commonly these ants are known as honey pot ants. Also, according to some authors these ants act as living storage vessels. The ant inside the nest, who is in need of food is used to strike the antennae of the honey pot ant, causing the honey pot ant to regurgitate the stored liquid from its storage organ. This kind of behavioural adaptation in ants is pronounced in the species living in the arid regions of North America, Africa and Australia. In every group some workers, called “repletes” remain in the nest and act as living vessels (Conway 1986)^[7]. Thus, the process of development of liquid food retrieval strategy shaped the cooperative attitude of collection of liquid food drops individually to store in the container of the honey pot ant who is extremely adapted to act as a pot to contain food to ensure sustainability of the colony members - an example of proximate cooperation to keep the social harmony in the ants.

By the by recent studies by Fujioka *et al.* (2022)^[14], exhibited, perhaps the climax of liquid food retrieval mechanism developed by the ant *Diacamma cf. indicum* where the worker ants are adapted to transport fluids with a riskier behaviour - holding a drop of liquid between the mandibles through surface tension- after which the ant shares this droplet with nest mates without ingestion or regurgitation in a behaviour called pseudo trophallaxis. This indicates that the ants are able to optimise the liquid-collection strategy depending on food quality and biophysical properties.

Moreover, in ants, to ensure feeding of the colony members, an effective cooperative behaviour is well evident. That is, the process of trophallaxis and/ or pseudo trophallaxis. In trophallaxis mutual exchange of regurgitated liquids between adult ants or between their larvae is ensured. Also some ants feed through mouth to anus. The food stored in the worker ants' social stomach passes through the abdomen rather than being regurgitated. So, cooperative attitude in

feeding or food retrieval in ants is well marked. But, interestingly, ants succeeded to develop another type of food retrieval device by holding the drop of liquid as stated above, is shared by colony members through pseudo trophallaxis.

Thus, it can be said that the ants have developed the art of retrieving the liquid food by different means depending on the ability to apply the organs in an effective way to ensure the success of such behaviour. To summarise the liquid food retrieval mechanisms the model presented in Fig. 1 marked with A, B and C could be taken into account.

Retrieval devices for solid food

Ants' solid foods varied to a great extent. They collect fruits, seeds, grains, sugar particles, sweets, insects/ insect-larvae, pieces of fish, meat, even salts from different sources in their foraging grounds (Burchill *et al.* 2022)^[4].

Usually, ants forage at large here and there for foods. They are habituated to carry self-manageable food particle alone (Fig.1 model D, E and F) but need cooperative transport (Fig. 1 model G, H, I, J, K, L) for heavier as well as self unmanageable food items to the nest. However, retrieval of solid food items is affected by different devices depending upon the decision taken by the worker ants in respect to a target food item to be procured to satisfy the need of the colony members. Thus, the solid food retrieval behaviours are of following types

a. Food transportation behaviour by a single worker ant

Usually, irrespective of species worker ant when decides that the available food particle is self manageable to carry the same alone to the nest, holds the same tightly by the mandibles and starts walking towards the nest, lifting the food item high up. (Fig.1 model A).

Also, in many cases, when the food item is much heavier to holding high up the concerned ant try to carry the same by dragging through pushing behaviour (Fig.1 model D) or pulling behaviour (Fig.1 model E).

b. Food transportation behaviour by ants in cases of self-unmanageable food items

In this case the ants are habituated to take the following decisions keeping in view of the food item in question.

1. The food item which one is not crackable

After coming in contact of this type of food the worker ant waits for the arrival of another one. If the said food item is manageable by the two ants then they try to carry the same cooperatively to the nest. They may carry the same by pushing and pulling system (Fig.1 model G and H) jointly but occasionally changing their position from pusher to puller.

But, in cases when the food item is heavier and/or variously shaped and the same is unmanageable by two workers assemblage of required number foragers is inevitable to carry the same cooperatively, in some species. The food transporting behaviour may be of (1) two ants pushing and one ant pulling (Fig.1 model I) or (2) two ants pushing and two ants pulling (Fig.1 model J), or (3) more than two ants pushing and more than two ants pulling (Fig.1 model K), or (4) some ants pushing from the back portion as well as from the side portion of the food while some could be seen acting as puller from the front end (Fig.1 model L). The number of pusher and puller ants varied to a great extent depending on the size or weight of the food item, the nature of surface of food transporting passage and the size of individual of the concerned ant species (Fig.1 model M). In other instance the workers are adapted to carry the solid as well as soft bodied animal intact by lifting the same cooperatively by many workers (Fig.1 model N). In these models the number mentioned against an ant indicates the original attempt by that ant to take part in retrieval process either as puller or pusher. But on way when they failed to cross the hurdle, some of them are habituated to change their position as could be seen from the arrows shown in model N.

2. The food item is crackable and/or cuttable into pieces:

Here, the worker ants of certain species (*Monomorium*, *Solenopsis*, *Iridomyrmex*, *Pheidologeton*) after coming in contact of a large bodied food item decide not to carry cooperatively the said food item as such but to cut the same into pieces. The pieces may be of different sizes so that some pieces could be carried by a worker individual alone, or some could be transported cooperatively, by two or more workers depending on the size/weight of the said piece. The ants also applied any of the above-mentioned device as stated (Fig.1 model D to N) for solid food transportation to carry the same to the nest.

Interestingly, in other instance the worker ants coming in contact of a large bodied animal prey especially the insect larva, they cut the same into small pieces and desiccate these by creating an insect jerky. After sometime, these pieces are taken to the nest to store these in the mound immediately below the mound surface. In a stock pile, a few to hundred pieces may be seen. Just like seeds and other solid food materials the ants have also developed the art to store soft bodied food items in a befitting manner for using the same in future in need.

Discussion

It appears that the workers/foragers when come in contact of the food first decide, if the said food is acceptable, how to procure the same to the nest. Irrespective of food type, that is, liquid or solid the mechanism almost same though there exists no cooperative food transportation in case of retrieval of liquid foods but involvement of many workers in an organized way is very much pronounced. Because of said behaviour ants succeeded to retrieve the liquid food. The said device is modified for transportation of solid food where two or more than two ants participate in transportation of the food item cooperatively. In both cases the aim of the workers is to lodge the food into the nest. Being social insect ants have developed the system of storage of liquid food by developing a morph as honey pot ant where individual ants had the opportunity to store the food using the honey pot ant as container. On the other hand, individual worker carry the solid food and deposit the same in the storage site in the nest. This storage site is equivalent to the container of honey pot ant. Also some ant species have developed the stockpile inside the nest where they can store the collected solid food particles for future use by the colony members. Thus in view of the generalized process of cooperative food transportation in ants we are presenting here a modified (after McCreey and Breed, 2014) [26] process of food retrieval in ants (Fig.2).

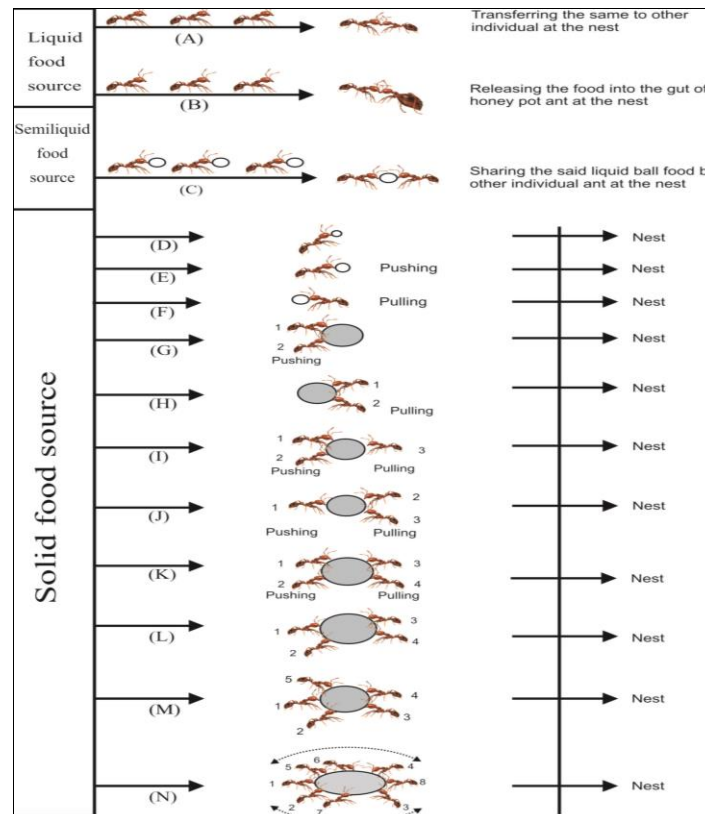


Fig 1: Development of possible sequential food- retrieval mechanisms in ants.

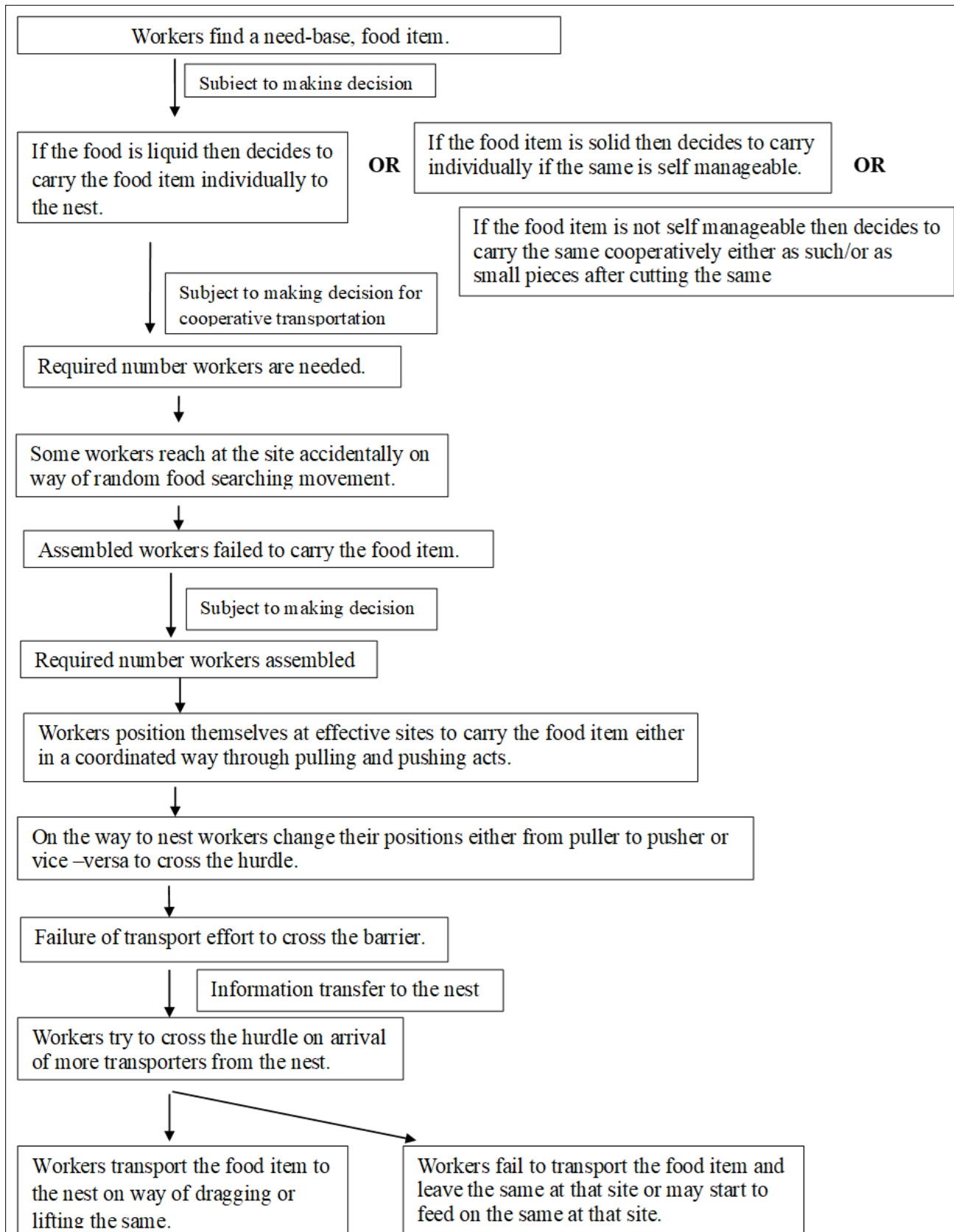


Fig 2: A schematic process of food retrieval mechanism in ants.

Inference

Irrespective of ant species and the foods they retrieved from the foraging ground it is almost clear that the food retrieval behaviours have evolved sequentially from a simple strategy to a complex strategy with a view to ensure the effectiveness of food - retrieval mechanism at the expense of less energy as far as possible.

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