Aims & Objectives

Aims
1. To provide information on the following topics in task partitioning: definition, relationship to division of labour, benefits and costs, taxonomic occurrence, patterns of material transfer, etc.

Objectives
1. Understand the relationship of task partitioning to division of labour in the organization of work in insect societies
2. Learn specific examples

Task Partitioning
Basic Information

Definition of Task Partitioning
TP is the division of a task into 2 or more sub-tasks
e.g. nectar collection & storage versus collection, storage

Division of Labour = Workers / Tasks
Task Partitioning = Task / Workers

Honey bees and stingless bees have task partitioning as above. Bumble bees so not. A nectar forager bumble bee also stores the nectar.
Ratnieks & Anderson. 1999. Insectes Sociaux

Task Partitioning
Task partitioning is the division of a task into two or more sub-tasks. If a load of forage is passed from one worker to another this is task partitioning.

In honey bees and stingless bees, a nectar forager transfers her nectar to one or more nectar receiver bees in the nest. This is similar to a “bucket brigade” or assembly line.

All known examples of TP involve the handling of material. The two sub-tasks are connected by the flow of material between them.

Many materials are transferred, especially forage and waste. Transfer can be direct, as in the honey bee nectar example, or indirect, as in *Atta cephalotes* waste disposal. Here, waste is transferred via a cache in the tunnel connecting a garden chamber to a dump chamber.

Ratnieks & Anderson. 1999. Insectes Sociaux

Direct Nectar Transfer in Honey Bee
receiver
forager
TP and DoL

Task Partitioning (TP) and Division of Labour (DoL) are two of the main ways that work is divided in an insect society. DoL has been studied more but recent study shows that task partitioning is very common foraging and waste disposal.

TP and DoL are not mutually exclusive alternatives. It is not TP or DoL. Frequently it is TP and DoL.

TP can actually cause greater DoL. In the honey bee nectar transfer example, the fact that nectar collection and storage are separate sub-tasks means that there can also be DoL, with a group of forager bees and a group of receiver bees. The receiver bees are younger bees. Later they will become foragers.

Ratnieks & Anderson. 1999. Insectes Sociaux

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Wood Pulp Collections & Building in Wasps

Vespinae: -TP
Same wasp forages & builds

Polistinae: Polybia: +TP
1 forager transfers to 2-4 builders

Polybia Swarm Building New Nest

Wasps can carry more wood pulp than they can actually build with. Having TP decouples foraging and building. As a result, wood pulp foragers can bring back a larger load of pulp, which they can transfer to several builders.

TP provides a clear benefit. Fewer foraging trips are needed. Foraging trips are energetically costly and also dangerous.

Honeydew Collection & Transport in Ants

1. Smaller workers “milk” honeydew secreting Homoptera
2. Direct transfer of honeydew to larger workers
3. Larger workers transport honeydew back to nest
Many Hemiptera (e.g. aphids, scale insects, plant hoppers) feed on plant phloem and excrete honeydew, which is rich in sugars. This is collected by ants, bees, wasps and some other organisms.

Ants must both collect honeydew from the insects and transport it. In Oecophylla weaver ants Formica wood ants smaller workers tend to milk the insects and then transfer the honeydew to larger workers for transport. Presumably it is energetically cheaper to do it this way. A small ant can probably milk an insect as well as a big ant but would not be as efficient at transporting liquid.

Here TP is again combined with DoL and makes use of the size differences among the workers.

Honeydew Collection & Transport in Ants

Leaf Collection in Atta

Leaves cut by *Atta laevigata* at Fazenda Aretuzina, Brazil, and which have fallen to the ground where they will be cut up into small pieces and taken back to the nest. Many cut leaves are wasted as they are not used.

Task Partitioning
Possible Benefits
Hygiene in Leafcutter Ants

*Atta* will cut leaves in trees and allow them to fall to the ground, where they are cut up and transported to the nest. By doing this a lot less walking, up and down trees, is needed. In one study on *Atta sexdens*, only about 50% of the leaves were retrieved. It is easy to cut leaves and leaves are abundant, so cutting excess leaves is a good strategy.

Atta Leafcutter Ants: Public Health

Fungus Garden
Weed Fungus: Escovopsis

Escovopsis fungus killer
Ascomycotina
Pathogen of fungus
Virulent
Destroys colonies

Weeding concentrates disease

Weed Fungus: Escovopsis

Escovopsis growing on waste dumped from Atta nest

Atta colonies face the challenge of keeping their colony and fungus gardens healthy. The garden fungus is susceptible to the weed fungus Escovopsis. This can kill the fungus garden which will kill the colony or entail very costly remedies such as building a new nest.

The ants have a whole series of defences against Escovopsis. They carefully lick and clean leaves brought into the nest. They weed the fungus garden and even groom individual strands of mycelium. They can direct more weeding to areas with Escovopsis. The worker ants also have an antibiotic bacterium growing on their bodies which kills Escovopsis. This gives the ants a whitish appearance. The workers also have a special gland, called the metapleural gland, which secretes disinfectant chemicals.

Sheffield research has shown that Atta colonies also have hygienic adaptations in the disposal of garbage. These include several behavioural and organizational features.
Hygienic Features in Internal Dumping

Separate garbage and garden chambers
Task partitioning
Division of labour
Exclusion of garbage workers from garden

TP & Hygiene in Atta cephalotes

*Atta cephalotes* can have massive colonies with many garden chambers in which their fungus crop is grown. These are connected to underground waste chambers in which the spent compost from the fungus garden and other waste is placed.

Workers working in the fungus garden take waste towards the garbage chambers. Few of them enter the garbage chamber. Instead, the waste is placed in a cache in the connecting tunnel. Workers living in the garbage chamber then take it the rest of the way.

This is another example in which TP and DoL are combined. The use of separate chambers, TP, and DoL effectively isolate the garbage chambers from the garden chambers. This is important as the waste may contain Escovopsis and other pathogenic micro-organisms.

Ants working in the garbage chamber are not allowed back into the garden chamber. Ants contaminated with garbage odour are aggressed or killed if they try to enter the garden chamber.

Hart & Ratnieks 2001a Behavioral Ecology & Sociobiology

Task Partitioning
Possible Benefits

Hygiene in Leafcutter Ants: *Atta colombica*

Foragers and garbage transporters are separate groups of workers. In other words there is division of labour. Most heap workers are former garbage transporters. Heap workers stay at this work.

Hart & Ratnieks 2002 Behavioral Ecology
Hygienic Features in External Dumping

Dumps downhill from forage entrances
Elevated dumping sites
Dumping into water
Opposite orientation of garbage and foraging trails
Division of labour
Task partitioning

Hygiene Insights from Atta Ants

Leafcutter ants do not rely on a single defence against weed fungi and diseases. Rather, they combine several defence mechanisms.

Antibiotics
+ worker behaviour
+ system organization
+ physical layout of nest chambers, dumping

Task Partitioning

Costs

TP involves material transfer. Therefore, time is wasted in:
transferring material
looking for a transfer partner
queuing for partner
delays occur even if balance is perfect because of stochastic variation in arrival rates
signalling to balance system (e.g., tremble dance)

Loss of material during transfer

Increased inter-individual contact
increased disease transmission?

Costs of Task Partitioning

Transfer costs can be reduced by caching
Caches can even out “supply” and “demand”

Problems:
Can’t cache liquids easily (although could have a wax nectar trough in bees?)
Cached materials might degrade (leaves dry out)
Cached materials might get lost or stolen
Still need balance between “cachers” and receivers

TP & Hygiene in Atta colombica

Atta colombica also has large colonies with many garden chambers in which their fungus crop is grown. But the waste is dumped externally.

There is division of labour between above ground workers. Foraging and garbage dumping are separate careers. Workers do not switch between these two activities. In addition, the garbage trail never leads in the same direction as the main foraging trail.

The workers who work on the garbage heap itself are former garbage dumpers.

The garbage dump is often below a convenient tree trunk or log to dump off. In this way the garbage dumping ants do not have to walk on the garbage dump itself. The garbage dump is always downhill to the nest entrance. Garbage is also dumped into a stream if one is nearby.

Hart & Ratnieks 2002 Behavioural Ecology
Costs of Task Partitioning

Task partitioning results in a more complex arrangement of work and introduces the problem of organizing the system to balance the work capacities of the various sub-tasks. That task partitioning occurs at all indicates that it must have substantial benefits, that are large enough to overcome these costs and more.

Task Partitioning Occurrence

TP is Taxonomically Widespread

TP occurs in Ants, Bees, Wasps, Termites
It must have evolved many times independently
TP can vary within a species for different forage materials
e.g. honeybees (nectar +TP, pollen –TP)
TP can vary between species for the same material
e.g. nectar: honeybee +TP, bumblebee -TP

Material Handling

| Into nest     | Liquids       | nectar, honey dew, water |
|              | Solids        | seeds, leaves, prey, wood pulp, propolis |
| Out of nest   | Solids        | garbage, excavated soil  |
| Inside nest   | Solids        | leaf pieces (in *Atta, Acromyrmex*) |

Ratnieks & Anderson, 1999, *Insectes Sociaux*
Anderson & Ratnieks, 2000, *Insectes Sociaux*

New Example

Fruit Cutting in Atta

Medium-Sized Workers Transport Cut Fruit

Task partitioning also occurs in fruit cutting in *Atta*. Large workers cut the fruit in order to cut larger pieces, and medium-sized workers carry the pieces back to the nest. Here TP allows DoL between large and medium-sized workers. Evison & Ratnieks 2007 *Ecological Entomology; Helanterä & Ratnieks 2008 American Naturalist.*
Task Partitioning

Types & Patterns of Transfer

Types of Transfer

Direct
Indirect
Direct & indirect
solids & liquids
solids
solids
Always at nest
flying workers (bees, wasps)
Also at food/on trail
non-flying (ants, termites)

Ratnieks & Anderson, 1999, Insectes Sociaux

Non-flying social insects may have foraging trails and so are more likely to meet each other outside the nest. It is probably for this reason that they may also transfer materials away from the nest.

Patterns of Transfer

Linear

Interlocking

Three Interlocking Cycles: Polybia wasps

The most complex pattern known involves three interlocking cycles. It occurs in Polybia occidentalis wasps (Vespidae: Polistinae: Epiponini) and probably in other epiponines. It also occurs in the British ant Lasius fuliginosus which builds a nest out of material it has collected. There are cycles of honeydew foragers, building material foragers, and builders.

Patterns of Transfer Apis Foraging

-TP
Pollen
placed directly into cells by forager

+TP
Nectar
transferred to storer bee in nest*
Water
transferred to storer bee in nest
Propolis
transferred to builder bee in nest

* occasionally, a nectar forager does not transfer (c. 1% foragers)

Atta Ants: Material Transfer

Hart, Ratnieks & Anderson, 2002

Hart, Ratnieks & Anderson, 1999, Insectes Sociaux
**Why Handle Pollen Without TP?**

Pollen foragers collect pollen in the pollen baskets. They are not unloaded by another bee but put the pollen directly into a cell by placing their legs in the cell and kicking the pollen off.

Transfer of pollen would probably be inefficient as it would take two receivers to unload one forager. That is, one to take each of the two pollen loads. This would presumably be carried in the receiver’s mandibles after transfer. It is not possible to transfer a pollen load from one pollen basket to another.

A pollen load is fragile and could easily break apart or be dropped during transfer. This is a second possible reason why pollen is not transferred.

**Why Handle Propolis With TP?**

Water is a liquid that is held in the forager’s crop and is transferred like nectar. A receiver extends her tongue and drinks from the forager’s mouth.

Propolis is a solid like pollen and is held in the pollen basket. However, it is subject to TP. A builder unloads a forager by taking the forager’s propolis in her mandibles. Why are pollen and propolis handled differently whereas water and nectar are not?

It is suggested that propolis is directly transferred because a forager cannot unload herself because the propolis is sticky. Propolis foragers can sometimes wait hours to be unloaded, if there is little demand for propolis.

**Hypothesis: Colony Size Task Partitioning**

<table>
<thead>
<tr>
<th>Nectar Collection &amp; Storage</th>
<th>+ TP</th>
<th>- TP</th>
</tr>
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<tbody>
<tr>
<td>Apis swarm-founded colonies</td>
<td></td>
<td>Bombus queen-founded colonies</td>
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<table>
<thead>
<tr>
<th>Wood Pulp Collection &amp; Building</th>
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<th>- TP</th>
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<tbody>
<tr>
<td>Polybia swarm-founded colonies</td>
<td></td>
<td>Vespula queen-founded colonies</td>
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**Colony Size & TP**

The simulation model shows that the stochastic delays in finding a transfer partner will be smaller in larger colonies. This suggests the testable hypothesis that TP will be more common in large-colony species.

The data support this prediction. Swarm-founding wasps and honey bees have TP in the handling of wood pulp and nectar, but Vespinae wasps and bumble bees do not. These species have colonies founded by a lone queen, so their colonies start small and often do not grow to large sizes.

In *Vespula* wasps there are also data to show that nectar is handled via TP in larger population colonies.

A trip to Merida, Yucatan, Mexico to study stingless bees provided additional support for the hypothesis. Five species were studied and all had TP in nectar collection. Stingless bees have swarm-founded colonies with colony sizes typically in excess of 1000 workers.

**Meliponine Research in Mexico**

Studied 5 species of stingless bees. All of them had TP. This supports the idea that TP is favoured by large colony size as all stingless bees have swarm-founded nests. That is, nests are always large.

Hart & Ratnieks. 2002. Ecological Entomology