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TASK PARTITIONING IN INSECT SOCIETIES: NATURAL HISTORY, ERGONOMICS, AND INFORMATION

Francis L.W. Ratnieks et Carl Anderson

Department of Animal and Plant Sciences, University of Sheffield,
Sheffield, S10 2TN, UK
et
Department of Ecology and Genetics, University of Aarhus,
8000 C Aarhus, Denmark

Résumé: La récolte et l'utilisation de ressources telles que la nourriture, l'eau et les matériaux de construction sont souvent divisées en plusieurs sous-tâches au cours desquelles les matériaux sont passés d'une ouvrière à une autre. Ce phénomène est qualifiée de division des tâches ("task partitioning"). Les liquides sont toujours transférés directement d'ouvrière à ouvrière, alors que les matériaux solides peuvent être transférés directement ou indirectement. Les transferts directs provoquent des files d'attentes puisque les ouvrières doivent trouver une partenaire réceptive. La simulation d'une tâche divisée en deux sous-tâches avec un transfert direct montre que le délai d'attente diminue à peu près exponentiellement quand la taille de la colonie augmente. Les abeilles domestiques et les guêpes *Polybia* recrutent des ouvrières durant ces délais, équilibrant ainsi les capacités de travail des groupes interagissant. Les ouvrières peuvent augmenter la qualité de l'information contenue dans les délais en faisant la moyenne sur plusieurs trajets ou en faisant plusieurs transferts par trajets. Les transferts multiples peuvent augmenter spectaculairement la qualité de l'information à un coût très faible, ce qui peut expliquer pourquoi ils existent chez l'abeille domestique où les fourageuses donnent fréquemment du nectar à plusieurs receveuses.

Mots-clés: *"task partitioning", délais d'attente, ergonomiques, information*

Abstract: task partitioning in insect societies
The collection and handling of colony resources such as food, water and nest construction material is often divided into subtasks in which the material is passed from one worker to another. This is known as task partitioning. Liquids are always transferred directly between workers whereas solids may be transferred either directly or indirectly. With direct transfer, queueing delays arise as workers search for a suitable partner. A simulation model of a two-stage partitioned task with direct transfer showed that queueing delays decrease roughly exponentially with colony size. Honey bees and *Polybia* wasps use these delays to recruit workers to balance the work capacities of the interacting groups. Workers can improve the quality of the information contained in these delays by averaging over consecutive trips or by multiple transfers per trip. Multiple transfer can dramatically improve information quality at surprisingly little cost, which may explain why multiple transfer occurs in the honey bee with foragers frequently giving nectar to several receivers.

Key-words: *task partitioning, queueing delays, ergonomics, information*

INTRODUCTION

The evolution of societies is the most recent of several "major evolutionary transitions" in the evolution of life on earth (Maynard Smith and Szathmáry 1995). In insect societies the subunits are individual organisms, whereas in multicellular organisms the subunits are cells. Viewed from the perspective of evolutionary transitions the study of insect sociality has broad relevance in biological research. Two major areas where this is especially true are in the study of conflicts among subunits and in the organisation of subunits. The organisation of insect societies is a vast topic of which the organisation of work is an important part (Oster and Wilson 1978; Pasteels and Deneubourg 1987). This article provides a brief introduction to one important aspect of work organisation: task partitioning. The article begins with basic information about task partitioning (definitions, examples). It then considers the costs and benefits of task partitioning, and finishes with a brief summary of the results of our recent simulation modelling of task partitioning with direct transfer. The modelling was carried out to investigate the effect of transfer delays on colony ergonomic efficiency and the reliability of the information content of these delays as an indicator of colony organisation.

Definition of Task Partitioning

Task partitioning is the division of a task that could be performed by one worker into two or more subtasks performed by different workers; for example, the collection and use or storage of one load of forage (Jeanne 1986a,b; reviewed in Ratnieks and Anderson, in press d). In contrast, division of labour is the division of the workforce among different tasks, with individual workers performing some subset of tasks for extended periods of time (Robinson 1992). That is, division of labour = workers / tasks and task partitioning = task / workers.

Task partitioning and division of labour are not mutually exclusive alternatives in the organisation of work. Both can occur at the same time and task partitioning can enhance division of labour (Jeanne 1986a; Ratnieks and Anderson, in press d). For example, in the honey bee division of labour occurs between nectar receivers and foragers, who are typically older bees. Division of labour between foragers and receivers can only occur because task partitioning has divided one task (collection and storage of a load of nectar) into two (collection, storage). Task partitioning can also occur without division of labour. For example, if honey bee workers performed either nectar storage or nectar collection and switched repeatedly between them there would be no division of labour but task partitioning would still occur. It seems that partitioning between builders and pulp and water foragers in the wasp *Polybia occidentalis* may fall into this category in that switching between builders and foragers is reported (Jeanne 1986b).

Implicit in the definition of task partitioning is the definition of a task. We consider a task to be a discrete unit of work that must be completed for the work to be completed. In foraging, the complete task is the collection, retrieval, and use or storage of a load of forage. Clearly, the task is incomplete if forage is collected but brought only part way to its point of use or storage. In foraging, the task is both unified and discretised from other tasks by the physical nature of the forage. In this sense the total work of foraging is composed of many tasks — the individual loads of forage being collected.

Examples of Task Partitioning

Figure 1 gives three examples of the collection of forage. The first shows the collection and storage of pollen by honey bee foragers. The forager collects the pollen and then places it

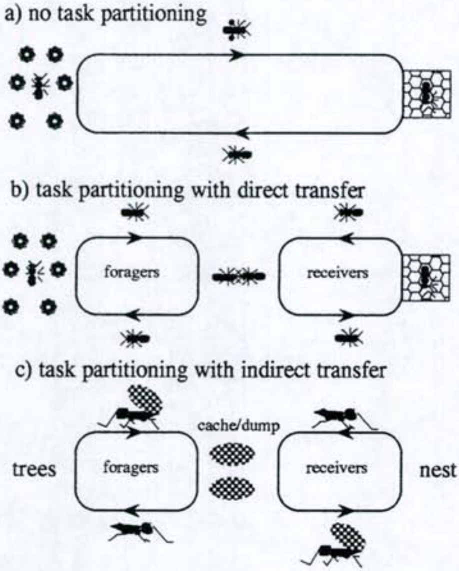

Figure 1: Three ways of organising the collection and storage of forage in insect societies, a) no task partitioning, b) task partitioning with direct transfer of material, and c) task partitioning with indirect transfer via a cache.
Figure 1: Trois manières d'organiser la collecte et le stockage de matér-iaux dans les sociétés d'insectes, a) pas de division des tâches, b) division de tâches avec transfert direct des matériaux, et c) division des tâches avec transfert indirect via un dépôt.

in a cell. Pollen collection in the honey bee does not show task partitioning because the complete task is performed by a single worker. The second example (Figure 1b) shows the collection and storage of nectar by honey bee foragers. Nectar is directly transferred between forager and receiver bees at the nest. The receiver then stores the nectar in a cell. Task partitioning occurs because the complete task, collection and use/storage of one load of forage, is performed by two workers. The third is also task partitioning but here transfer is indirect. The forage is placed on the ground which acts as a "cache".

OCCURRENCE AND BASIC FEATURES OF TASK PARTITIONING

Table 1 provides a summary of some basic features of task partitioning. Task partitioning occurs in ants, bees, wasps, and termites and our impression is that it is a common feature of foraging in insect societies. The only example of task partitioning not in foraging that we are currently aware of is in the excavation of nest chambers in *Pogonomyrmex* (D. M. Gordon, pers. comm.). This is an interesting exception, in that it still concerns material transport. Whether this is the "exception that proves the rule" and confirms that task partitioning is found only where materials are moved into and out of the nest, or whether task partitioning will also be found in tasks performed exclusively within the nest remains to be determined.

Whether transfer is direct or indirect depends on the physical properties of the forage. Liquids (water, honeydew, nectar) are always transferred directly whereas solids (prey, leaf pieces, seeds, soil) may be transferred directly or indirectly (Table 1). Wood pulp collected by wasps is also transferred directly, possibly because the small pellets collected are too easily lost if cached in the nest or blown away if cached on the outer surface of the nest, which is the transfer location in *P. occidentalis* (Jeanne 1996). Transfer can take place at the nest, at the forage site, or in between. In bees and wasps, which have

Material	Species	Mode of transfer		Location of transfer	Number of cycles
		Direct	Indirect		
Nectar	*Apis mellifera*	•		nest	2
Leaves	*Atta cephalotes*	•	•	trail	3 (L)
	Atta sexdens		•	trail	3 (L)
Grass stems	*Hodotermes mossambicus*		•	forage site	2
Honeydew	*Oecophylla longinoda*	•		forage site	2
Propolis	*Apis mellifera*	•		nest	2
Wood pulp	*Polybia occidentalis*	•		nest	3 (I)
Water	*Polybia occidentalis*	•		nest	3 (I)
Soil particles	*Lasius fuligonosus*		•	nest	3 (I)
Cocoons	*Polyergus rufescens*		•	nest	2
Insect prey	*Daceton amrigerum*	•		trail	2+ (L)
	Megaponera foetans		•	forage site	2
	Ectatomma ruidum	•	•	forage site	2
	Lasius fuliginosus	•		trail	many (L)
	Polybia occidentalis	•		nest	2
Seeds	*Messor*	•		trail	2+ (L)

Table 1: Some examples of foraged materials in which collection and storage or use is partitioned, and their mode of transfer, location of transfer and number of cycles (stages) involved. (L = linear arrangement, I = interlocking.)

Tableau 1: Exemples de matériaux récoltés où collecte et stockage, ou utilisation, sont divisées en phases (or sous-tâches), avec le mode de transfert, la localisation des transferts et le nombre de cycles impliqués. (L=arrangement linéaire, I=arrangement imbriqué).

flying workers, transfer always occurs at the nest. In ants and termites, which often have foraging trails and multiple workers at the collection site, transfer may occur at all three locations. Transfer may involve two or three groups of workers. When three groups of workers occur, transfer may be linear as in *Atta sexdens* (Figure 2) or interlocking, as in *Polybia occidentalis* in which pulp foragers transfer to builders and water foragers transfer to both builders and pulp foragers. Pulp foragers use water to moisten the piece of wood from which they remove pulp.

BENEFITS OF TASK PARTITIONING

The presumed major benefits of task partitioning fall into two main categories (Ratnieks and Anderson, in press d). In the first task partitioning capitalises on differences in the work ability of individuals. In the second task partitioning improves material handling efficiency.

1. Individual differences in performance When individuals vary in ability, task partitioning is a mechanism that can divide the task in such a way that individuals do what they are better at, thereby enhancing colony performance. For example, *Oecophylla* ants collect honeydew from scale insects. Smaller workers perform the milking and larger workers transport the honeydew back to the nest (Hölldobler 1984; Hölldobler and Wilson 1990). In *Daceton*, workers returning along a forage trail may transfer their load to other, faster walking, workers (Wilson 1971). In *Lasius fuliginosus*, some workers live in "outstations" (Dobrzańska 1966). Forage may be transferred between workers as it is retrieved. The presumed advantage is that workers familiar with the area near their outstation carry the

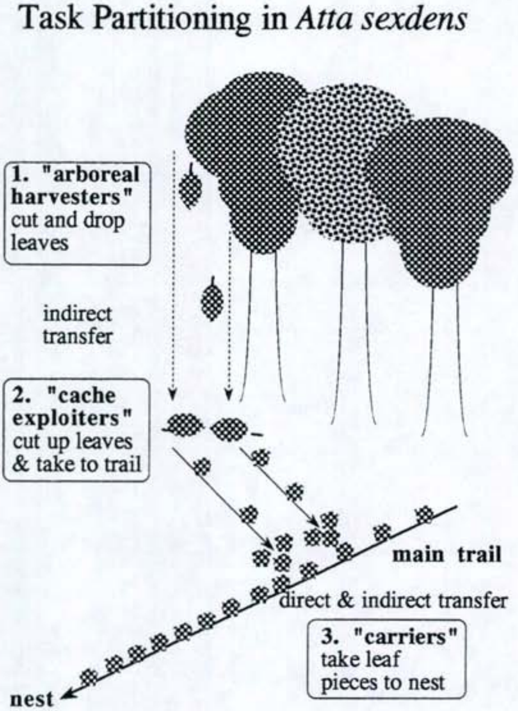

Figure 2: Task partitioning in Atta sexdens, an example of a three-stage partitioned task with two caches.

Figure 2: Division des tâches chez Atta sexdens, un exemple de tâche divisée en trois sous-tâches avec deux dépôts.

forage through their area more rapidly and safely. The first two examples depend upon morphological differences among workers and the final one on differences in worker experience.

2. Enhanced material handling Under some circumstances task partitioning reduces the total amount of work to be performed. In *Atta sexdens* dropping of leaves by "arboreal harvesters" and their retrieval by "cache exploiters" (Figure 2; Fowler and Robinson 1979) reduces the amount of walking needed. In *P. occidentalis* a wood pulp forager can collect sufficient pulp for approximately three builders, so that partitioning reduces the number of foraging trips needed per unit of building (Jeanne 1986b).

COSTS OF TASK PARTITIONING

There are also numerous potential costs to task partitioning (Ratnieks and Anderson, in press d). The most obvious of these are the time costs in transfer. Time can be wasted transferring, and also in searching and queueing for a transfer partner. These time costs are especially relevant to direct transfer. With indirect transfer the cache can eliminate or greatly reduce queueing and searching time costs. An additional cost that may in some cases arise directly from transfer especially indirect transfer, is loss of material. Where task partitioning occurs there will usually be a need to adjust the relative numbers of foragers and receivers because of death of foragers and changes in the ease with which forage is collected.

By introducing a series arrangement in the organization of workers task partitioning also reduces the reliability of an insect colony (Ratnieks and Anderson, in press d). However, the reduction in reliability is probably of insignificant magnitude especially in large colony species where literally thousands of foragers and receivers each work in parallel.

Looking at individual species and the materials they collect it can be seen that the collection of one material may be partitioned but another may not as in nectar and pollen collection in the honey bee (Table 2). This may be because of material-specific costs and benefits of transfer. Why is pollen not transferred by honey bees? Possibly because the pollen pellet would sometimes be dropped and because two receivers would be needed for each forager, assuming that the receiver would carry the pellet in her mandibles. Like pollen, honey bee foragers also transport propolis in the pollen baskets on their hind legs. But here the propolis is transferred to a receiver. It is suggested that this occurs because a propolis forager is unable to unload the sticky propolis herself (Ratnieks and Anderson, in press d).

Species	Transfer?	
	Yes	No
Apis mellifera	nectar, water, propolis	pollen
Bombus		nectar, pollen
Polybia occidentalis	prey, nectar, water, wood pulp	
Vespula	prey, nectar	water, wood pulp, nectar

Table 2: In a given species, which forage is transferred?
Tableau 2: Quels matériaux sont transférés dans une espèce donnée?

SIMULATION MODELLING OF TASK PARTITIONING

Queueing delays in obtaining a transfer partner are inevitable when direct transfer of forage occurs. When the relative work capacities of the forager and receiver groups are out of balance the group in excess will wait longer for partners. But even when the work capacities are equal delays will still occur because of stochastic fluctuations in the arrival of receivers and foragers at the transfer area. These queueing delays are of importance. They have the potential to reduce colony efficiency. In addition, the queueing delays are used by honey bees in recruitment and by *Polybia* wasps in task switching.

SIMULATION MODEL

Using a continuous time stochastic computer simulation we modelled a two-stage partitioned task with direct transfer, as in honey bee nectar collection and storage. Full details of the model are given in Anderson and Ratnieks (in press a). Figure 3 shows the basic schema for the model. Foragers with a full nectar load and empty receivers pair at the nest and transfer. When queueing occurs the queueing discipline is "serve in random order". Each worker then makes another foraging or storage trip before returning again to the transfer area. The durations of each foraging or storage trip were randomly taken from a distribution with specified shape, mean, and variance (typically normally distributed with mean and variance of 500 time units). Transfer durations were also randomly taken from a distribution (typically normally distributed with mean and variance of 50 time units). The number of foragers and receivers could also be varied. Queueing delays occur and these are the primary data derived from the simulation.

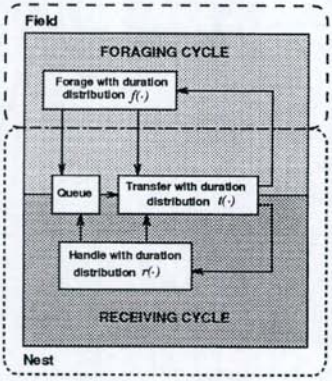

Figure 3: The foraging / receiving cycle used in the simulation model.
Figure 3: Cycle de fourragement / réception utilisé dans le modèle.

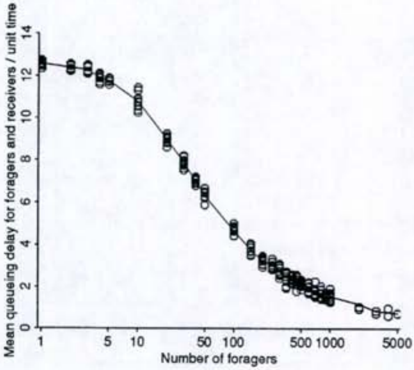

Figure 4: Effect of colony size on mean queueing delay.
Figure 4: Effet de la taille de la colonie sur la durée moyenne d'attente.

RESULTS: ERGONOMICS

Figure 4 shows the effect of number of foragers (note: there are also an equal number of receivers) on the mean queueing delay for foragers and receivers. The amount of time lost in queueing decreases as colony size increases. This is because as colony size increases the stochastic fluctuations in arrival rates of foragers and receivers at the transfer area reduce. The results clearly show that the queueing delays in a large colony with thousands of foragers are only about 10% of the maximum. Queueing delay is halved at a colony size of approximately 50 foragers.

These data suggest that task partitioning with direct transfer is more likely to occur in large colony species, because the time cost caused by queueing delays will be relatively large in small colony species. Empirical data support this hypothesis (Figure 3). Transfer of nectar occurs in the honey bee but not in bumble bees (Tables 2 and 3). Transfer of wood pulp occurs in *Polybia* but not in Vespinae wasps. Both honey bees and *Polybia* have swarm-founded colonies, so colonies are never small. In contrast both bumble bees and Vespinae have colonies founded by a single queen. Similarly, nectar transfer occurs in large but not in small colonies of *Vespula*.

RESULTS: INFORMATION

When the work capacities of the forager group and the receiver group are not equal the group in excess will experience longer queueing delays. If the colony could monitor all the queueing delays the optimisation of the foraging system would be simple. The group experiencing longer delays would need more recruits, or alternatively some of the group experiencing shorter delays could switch tasks. However, unlike human society, social insects probably have no mechanism for the central collecting of information. Instead, individual workers must make decisions about recruitment and task switching based on their own experience. Returning nectar foragers that experience a short queueing delay

Species	Colony size	Swarm-founded?	Transfer?	
			Yes	No
Apis mellifera	25,000 (max=80000)	yes	nectar	
Bombus	100–400 (max=2183)	no		nectar
Polybia occidentalis	50–400 (max=598)	yes	wood pulp	
Vespula	$\approx$ 1000 (95–5207)	no		wood pulp
Vespula (old colonies)	large	no	nectar	
Vespula (young colonies)	small	no		nectar

Table 3: Colony founding method and size and whether material is transferred for a variety of species and materials.
Tableau 3: Mode de fondation des colonies, taille des colonies et existence de transferts de matériaux pour diverses espèces et matériaux

Transfer delay	Cause	Action	Recruits
Short	too few foragers	waggle dance	more foragers
Medium	close to optimum	no dance	no recruits
Long	too few receivers	tremble dance	more receivers

Table 4: Honey bee foragers: transfer delay and recruitment behaviour.
Tableau 4: Délai d'attente et comportement de recrutement chez les fourrageuses d'abeille domestique.

tend to perform a waggle dance thereby recruiting more foragers and those that experience a long delay tend to perform a tremble dance which increases the number of receivers (Seeley 1995; Table 4). Typically there is no recruitment if workers experience intermediate delays. In essence, each individual worker needs to estimate the true mean queueing delay from her own experience. However, given stochastic variation in queueing delays the information available in any single delay is quite unreliable (Ratnieks and Anderson, in press a,c). Information quality can be increased in several ways. One method is only to use the reliable portion of the queueing delay information. These are the long delays experienced by the group in excess. Short delays do not give reliable information because a short delay may come about because an excess-group-worker is simply lucky in the "serve in random order" queueing discipline. (We think it unlikely that social insects can queue, as do the English, "first come first served".) Another method is to average over trips. Nectar transfer in the honey bee typically involves multiple transfer per foraging trip (Kirchner and Lindauer 1994; Seeley 1995). That is, a forager unloads nectar to several receivers on returning to the nest. There is no satisfactory explanation for this, but we hypothesise that it is to obtain additional information about queueing delays. Essentially, a forager can obtain several estimates per return to the nest. Figure 5 shows that multiple transfer does result in more reliable information, as shown by the reduced standard deviation of mean queueing delay. Quite unexpectedly the simulation also shows that the total queueing delay is little affected by multiple transfer. Figure 5 shows that, for 500 foragers, an increase in total queueing delay per trip of only $2\frac{1}{4}$ units as the number of transfers increases from one to six per trip. Not the 600% increase (10 units) that we initially expected. The low increase comes about because multiple transfer also increases the rate at which foragers and receivers seek partners. The data in Figure 5 are for a simulation in which the work capacities of the forager and receiver groups are matched.

When the work capacities are not equal the increase in total transfer duration due to multiple transfer reduces even more.

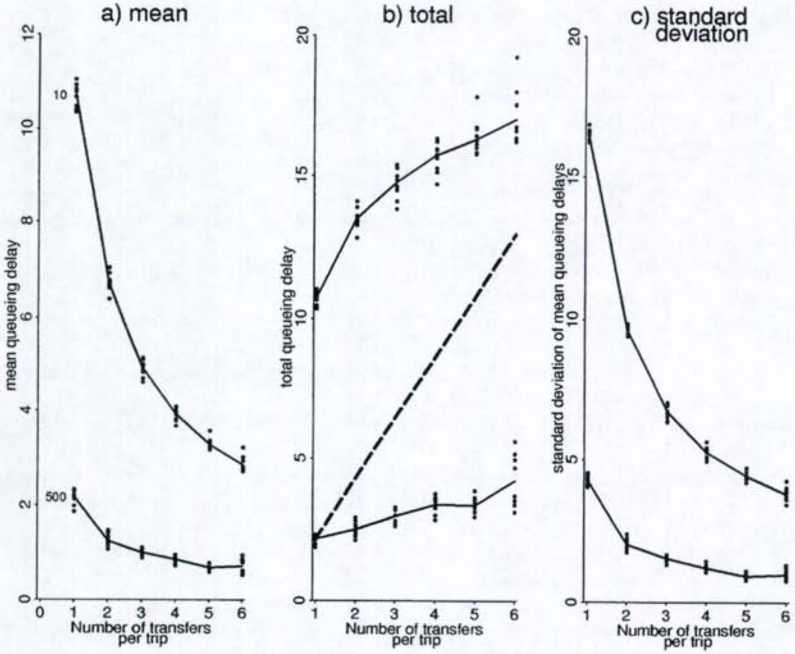

Figure 5: Effects of multiple transfer for small (10 foragers) and large (500) colonies. a) mean queueing delay for an individual trip and b) the total queueing delay (mean delay × number of transfers). c) reduction of standard deviation of delays with number of transfers per trip. The dashed line in b) shows the expected total delay if the dynamics were unaffected by multiple transfer.

Figure 5: Effets de transfert multiples pour des petites et grandes colonies (10 et 500 fourrageuses). a) délai moyen d'attente pour un trajet et b) délai total d'attente pour un trajet (délail moyen × nombre de transferts). c) réduction de la variation des délais (écart-type) avec l'augmentation du nombre de transferts par voyage. La ligne pointillés en b) montre le délai total attendu si la dynamique n'etait pas affectée par les transferts multiples.

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