# Haplodiploidy seems to facilitate queen re-absorption and dependent founding in eusocial insects

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**Eusociality, independent founding, permanently sterile helpers, swarm-founding**

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**Since haplodiploid sterile workers are more closely related to their sisters than diploid sterile workers are to theirs, haplodiploid sterile workers are more likely to help their reproductive sisters while occupying new places, and keep these places occupied through re-absorption of outbreeding queens. A brief overview of such behavioural patterns in wasps, bees, ants and termites supports this idea. The argument put forward is that rather than explaining eusociality itself, haplodiploidy explains why many haplodiploid social insects, given their queen re-absorption and dependent founding, are so successful in dominating a wide range of niches.**

## Diploid and haplodiploid species

In diploid species, such as termites and humans, each sex has two sets of chromosomes, one from each parent. In contrast, in haplodiploid species like the Hymenoptera (wasps, bees, ants), females have two sets of chromosomes, one from each parent, and are diploid, while males arise from unfertilised eggs, have only one set of chromosomes, and are haploid (Trivers 1985: 177). As a result of this, in a haplodiploid species, under outbreeding, the degree of relatedness between a sterile worker (which is female) and her fertile, reproducing sister is ¾. However, in a diploid species the degree of relatedness between a worker, which can be both male and female in termites, and the reproducing female is ½. Stated differently: 'It is well known that a singly inseminated hymenopteran foundress generates a colony in which sisters share ¾ of their genome with each other, ¼ with their brothers, and ½ with any offspring they might have. Sociobiologists have often thought that this genetic asymmetry is causal in the evolution of eusociality in the Hymenoptera (see Andersson 1984)' (Reilly 1987: 393). This last idea seems to be somewhat disputed by the fact that there are haplodiploid (wasps, bees, ants) as well as diploid (termites) eusocial species with complex societies including castes of permanently sterile workers. As Alexander *et al*. (1991: 7) write: 'Haplodiploidy, (....), is neither necessary nor sufficient to account for the appearance and maintenance of eusociality'.

Here I argue that the difference between haplodiploidy versus diploidy might be causal in the evolution of different strategies employed while colonizing new places and keeping these places occupied.

## Two strategies to colonize new places

Virtually every place on earth capable of sustaining living organisms is occupied by species exploiting those niches. Furthermore, places are constantly contested by new colonizers, trying to establish themselves. In social insects, one can visualize two different, opposing strategies for starting a colony. In the first strategy, a single fertilized female, or a mated pair, finds a sheltered place, hide away, and slowly starts a colony. The second strategy is almost the opposite: A fertilized female leaves the natal colony accompanied by an army of helpers. Right from the start the new colony consists of a large and strong family group.

Individuals of many diploid social species collectively conquer, occupy and defend new territories. For instance, there are border-clashes between clans of spotted hyenas (e.g., Kruuk 1972), or between communities of chimpanzees (e.g. Goodall 1986). However, as will be discussed below, a female of a diploid species arriving at a new territory with a group of sterile workers and occupying it is apparently unknown. By contrast, haplodiploid social insects often establish new colonies by swarm-founding or what here will be called 'dependent founding'. The best known example is perhaps a swarm of honeybees leaving the hive in an attempt to start another colony.

This is the moment to address a semantic issue. Two distinctly different phenomena are sometimes both called ´swarming´. Here, *independent founding* is used to refer to a single queen (in termites accompanied by a reproductive male) who attempts to start a colony without the help of workers. When numerous males and females of one species leave several nests at about the same time for the nuptial flight, this may create a 'swarm'. *Dependent founding* is here used to describe an attempt to found a new colony by a (large) group of workers and one or more queens (Aron & Passera 1999). In literature about wasps and bees, dependent founding is usually called swarm-founding.

**1.** A nest of the wasp *Parachartergus fraternus* in Costa Rica. Photo: Robert L. Jeanne
**1.** Een nest van de wesp *Parachartergus fraternus* in Costa Rica.

## The hypothesis at issue

As will be briefly reviewed below, in many haplodiploid, but apparently in no diploid eusocial insects, dependent founding and queen re-absorption occurs. I argue that this relates to the particular differences between the two. Specifically, in haplodiploid eusocial insects, if a daughter of the founding queen outbreeds – that is, mates with a male from another colony – her sterile daughters are more closely related to her offspring than in diploid eusocial insects. With Hamilton's (1964) publication in mind, it is therefore expected that compared to workers of haplodiploid species, diploid workers are less willing to care for offspring of an outbreeding female. But for diploid sterile workers there is another opportunity to maximize the number of copies of their genes in the next generation, namely to concentrate on maximizing the number of alates (winged reproductives). One way to achieve this is rejecting the return to the nest of outbreeding females, and instead supporting inbreeding reproductive brothers and sisters, who will also produce alates

So diploid sterile workers are more likely to (i) concentrate on producing alates instead of investing in the offspring of outbreeding reproductive sisters, and (ii) promote inbreeding (eventually leading to the demise of the colony) instead of adopting outbreeding sisters. In contrast, haplodiploid sterile workers are more likely to (i) assist their reproductive outbreeding sisters while founding new colonies (dependent founding), and (ii) re-absorb queens in their own existing nest. With queen re-absorption there is no inherent limit on group longevity, so places could in principle be kept occupied indefinitely.

Thus the expectation is that haplodiploid eusocial insects more often show dependent-founding and queen re-absorption than diploid eusocial insects. In order to evaluate this hypothesis, different groups of eusocial insects will now briefly be reviewed.

## Wasps

Independent-founding wasps initiate new nests as lone females who may later be joined by cofoundresses. Dependent founding species are largely restricted to the tropics, though a few of such wasps range into the subtropics. They initiate new nests in coordinated groups of queens (reproductive females) and workers, and avoid many problems experienced by independent founders when they initiate a new colony. Among the advantages of dependent founding is a reduction of the loss of many reproductive adults (Bouwma *et al.* 2003). Wasps of the tribe Epiponini, a successful group of about 200 neotropical species, are characterized by multiple queens. Hastings *et al.* (1998: 574) remark about the large-colony epiponine wasp, *Brachygastra mellifica* (Say): 'Queens have never been seen to found nests independently or to insinuate themselves into other colonies'. The epiponine wasp *Parachartergus colobopterus* (Lichtenstein) is also a good example of dependent founding wasps (figure 1 depicts the nest of a congeneric wasp species). Strassmann *et al.* (1997) found that colonies requeen on average once every 9-12 months. Individual colonies are long-lived, lasting an average of 347 days, with a maximum of over 4.5 years.

In their study of the epiponine wasp *Ropalidia revolutionalis* (de Saussure), Henshaw *et al.* (2004: 469) report that 'Swarm-founding [thus dependent founding] colonies have many more queens than independent-founding colonies, which should dramatically reduce relatedness, posing a challenge to cooperation. However, in each instance, swarm-founding species have also evolved a cyclical pattern of queen reduction which elevates relatedness despite high queen numbers'. Howard *et al.* (2002: 365) write: 'The ability of swarms to emigrate and found new nests has enabled the 20 genera of the polistine tribe Epiponinito to become the ecologically dominant eusocial wasps of the New World tropics (Jeanne 1991)'.

## Bees

Bees can be loosely characterized as wasps that have specialized on collecting pollen instead of insect prey as larval food (Wilson 1975: 428). 'At the risk of oversimplification, it can be said that the key to understanding the biology of the honeybee lies in its ultimately tropical origin. It seems very likely that the species originated somewhere in the African tropics or subtropics and penetrated colder climates prior to the time it came under human cultivation. Thus, unlike the vast majority of social bees endemic to the cold temperate zones, the honeybee is perennial, and, being perennial, is able to grow and sustain large colonies. Having large colonies, it must forage widely and exploit efficiently the flowers within the flight range of its nest, the waggle dance and the release of scent from the Nasanov gland of the abdomen are clearly adaptations to this end' (Wilson 1975: 431-2). In a honeybee *Apis mellifera* Linnaeus colony, there usually is only one queen, but temporarily there are multiple queens present when virgin queens are reared for reproductive swarming or queen replacement (Schneider *et al.* 2001). Honeybee queens are polyandrous, mating with fourteen males on average. The natural process of reproduction by fission results in a daughter colony composed mainly of older workers

**2.** Nest mounds of *Formica polyctena* are often the result of budding and may therefore be situated in close proximity of each other. Photo: Jinze Noordijk
**2.** Koepelnesten van *Formica polyctena* komen vaak door 'budding' tot stand en liggen vervolgens vaak vlak naast elkaar.

(Chapman *et al.* 2007). The primary swarm leaves the nest with the mated mother queen. Further 'after-swarms' can leave the nest; these are composed of virgin queens and sister workers (Kryger & Moritz 1997).

## Ants

With anst (Formicidae), young queens can found new colonies independently, without the help of workers, or dependently, with the help of workers (Aron & Passera 1999). In army ants and some other species the queen is wingless, never leaving her colony, and males fly between colonies to mate (Hölldobler & Wilson 1990: 153, see also Kronauer *et al.* 2007). This implies that these species always found new colonies dependently. In most ant species though, queens do have wings. During and following the nuptial flight, the vast majority of them is killed by a variety of predators, including workers of their own species. Some succeed in founding a colony independently, but if a queen stays or lands near her own colony, she may be absorbed by the home nest (Hölldobler & Wilson 1990: 210). 'The coexistence of two or more mated and potentially breeding females within a colony (polygyny) is common in social Hymenoptera, and especially among ants (Holldobler & Wilson 1977, Keller 1995). The permanent coexistence of queens, also known as secondary polygyny, arises through the adoption of reproductive queens into mature colonies' Hannonen (2002).

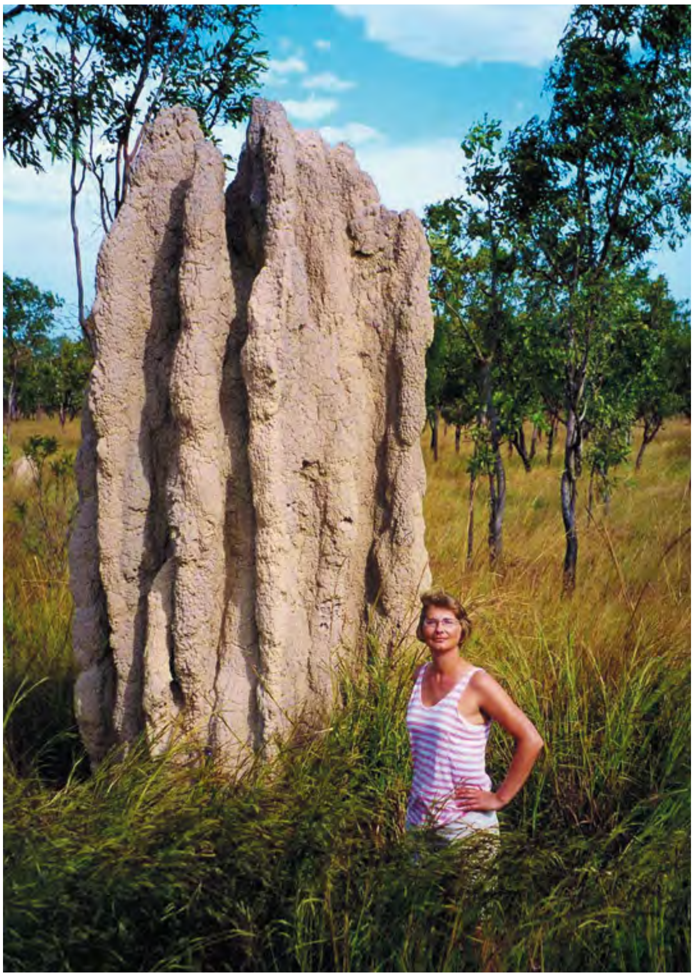
In many species there is colony division through budding, during which the queen may be carried by workers (Hölldobler & Wilson 1990: 177). 'Workers from mature colonies of the Australian meat ant *Iridomyrmex purpureus* (Smith) often join newly inseminated queens and help them excavate their first nest. As a result, satellite colonies are founded around the periphery of the older established nest' (Hölldobler & Wilson 1990: 210). Other examples of dependent founding in ants, so effective that they are often considered pests, are the pharaoh ant *Monomorium pharaonis* Linnaeus and argentine ant *Linepithema humile* (Mayr). Another well-known and conspicuous example from European and Russian forests is *Formica polyctena* Foerster; new nest mounds are often created by budding and may lie in close proximity of each other (figure 2).

Queens in a colony may also be replaced by daughters: 'Queen replacement has (…) been recently shown to occur in monogyne colonies of the fire ant *Solenopsis invicta* (DeHeer & Tschinkel 1998)' (Keller 1998: 236).

For a long time it was widely held that the ant *Carebara vidua* displayed a spectacular form of dependent founding, in which a few minuscule workers clung onto the enormous virgin queen during the nuptial flight from the nest and assisted her, once she had mated, in founding a new colony. This idea was fed by the fact that there exists a huge size dimorphism between workers and queens. However, this attractive story is dispelled by Robertson and Villet (1989) as a myth.

## Termites

The termites (Isoptera) form a diverse group with over 2600 described species (Korb 2008: 152), all of which are eusocial (Pamilo 1991: 79). A termite colony (figure 3) gradually originates from a single pair of reproductive swarmer termites; the king and queen. They are monogamous and in contrast to the Hymenoptera, copulate for the first time after having secured a nest (Wilson 1975: 435). Other individuals within the colony, called secondary reproductives or neotenics, may develop functional reproductive organs. These secondary reproductives have no wings, and they never disperse or outbreed (Thorne 1997: 30). Numerous neotenics can contribute to overall egg production in a colony, hence exceeding many times the egg production of the single primary reproductive queen. Although two or three unrelated female reproductives in the same colony have also been reported (Bulmer *et al.* 2001), because sometimes several queens found a colony together (Thorne 1983), and a colony may fission when their tunnels become very long, all colony-members usually descend from one 'tandem-running' outbreeding pair. Mate-seeking adults (alates) tend to avoid forming partnerships with nest mates (Shellman-Reeve 2001). Reilly (1987: 347) concludes that colonies of the termite *Reticulitermes flavipes* (Kollar) are inbred and genetically isolated from nearby colonies. She also writes: 'These results differ somewhat from published accounts of the eusocial Hymenoptera, in that measurements of population structure in the Hymenoptera



**3.** A termite mound in Australia. Photo: F.J.S. Weeda
**3.** Een termietenheuvel in Australië.

do not generally suggest the action of inbreeding'. Despite secondary and even tertiary inbred reproductives, individual colonies appear to be mortal (Wilson 1975: 436-7).

It is noteworthy that in transference experiments, termites seem more hostile to foreign queens than are ants, bees or wasps (Hamilton 1972: 197), suggesting that in termites queens are never re-absorbed. Swarm or dependent founding is apparently unknown in termites.

Due to the cryptic nature of their habitats, almost nothing is known about dependent founding and queen re-absorption in other groups of diploid eusocial species, such as the 'snapping shrimp' *Synalpheus regalis* Duffy (see Duffy 2002) and the 'ambrosia beetle' *Austroplatypus incompertus* (Schedl). Smith *et al*. (2009: 285) remark about the latter: 'Galleries initiated by a solitary fertilized female are later inhabited by overlapping generations'.

## Concluding remarks

At least at first sight, it seems that dependent founding and queen re-absorption are absent in termites, but often found in the Hymenoptera. Such is expected since sterile workers, when permanently sterile, face a different window of opportunity in haplodiploid species compared to diploid species. In haplodiploid species sterile workers often prefer to invest in the offspring of outbreeding sisters, while in diploid species there is a preference for maximally producing alates – that is reproductive brothers and sisters, inbred nephews and nieces, and so on – instead of investing in the offspring of these alates. In other words, the higher relatedness values under haplodiploidy lower the barrier to dependent foundation and queen re-absorption in eusocial insects with permanently sterile workers. Dependent founding – allowing immediate formation of a full-fledged society – and queen re-absorption are perhaps especially advantageous in the tropics, where niches are contested year-round. These strategies bring with them a superior ability to quickly, aggressively and collectively occupy new places, and keep them occupied. Certainly, many species of Hymenoptera employ independent founding only, and many others show a mixture of dependent and independent founding. But, at first sight at least, it would appear that the hypothesis expressed in the title holds.

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## Samenvatting

**Haplodiploïdie lijkt de heropname van koninginnen en gezamenlijke kolonie-stichting bij eusociale insecten te begunstigen**

Aangezien haplodiploïde steriele werksters nauwer verwant zijn aan hun vruchtbare zusters (‘toekomstige koninginnen’) dan bij diploïde soorten het geval is, zijn ze eerder geneigd om koninginnen te helpen nieuwe kolonies te stichten of het territorium bezet te houden door na de paring koninginnen terug te laten keren tot de kolonie. Een beknopt overzicht van gedragsverschijnselen bij beide type verwantschappen in wespen, bijen, mieren (alle drie haplodiploïd) en termieten (diploïd) ondersteunt dit idee.

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