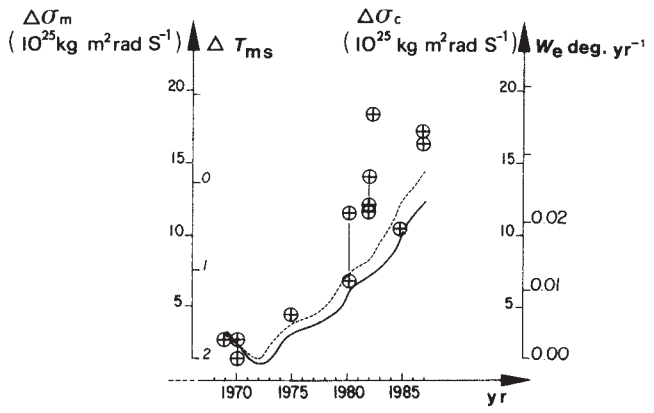

Fig. 3 Changes in the angular momentum of the mantle and of the core for the recent epoch (1969–1987). Solid line, $\Delta\sigma_m$ (see text) or ΔT (in ms); broken line, $\Delta\sigma_m$ (or ΔT) corrected from the secular decrease in length of day T; ⊕, estimates of $-\Delta\sigma_c$.

increasing dissymmetry from 1965 to 1940 forbidding the strict application of formula (3); it could be because of the poor quality of the corresponding SV models (in particular the earlier models are based on very few observatories in the South Hemisphere (see Fig. 2 of Langel *et al.*[17])). Nevertheless, the estimates of $\Delta\sigma_c$ before 1970 remain fairly well correlated with the estimates of $\Delta\sigma_m$; in particular we observe a decreasing trend of $(-\Delta\sigma_c)$ before 1970. Decade changes in the mantle angular momentum as observed during the past 20 yr can be balanced by a flow made of cylindrical axial annuli and compatible with the values computed at the CMB from SV data. The phenomenon responsible for the (differential) westward drift of the geomagnetic field would then be a genuine motion of fluid and not a MHD wave propagating westwards. In this paper we have only described the global budget of angular momentum; it is now necessary to study the exchange and coupling mechanisms both inside the core[27] and between the core and the mantle[30].

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Genetic determination of guarding and undertaking in honey-bee colonies

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Darwin[1] considered the dramatic differences in morphology and behaviour among sterile workers, the basis of colony division of labour in the social insects, to be a greater challenge to his theory of natural selection than the occurrence of worker sterility itself. Darwin's model for the evolution of these worker traits required: (1) heritable variation among workers within colonies; (2) variation in reproductive success among colonies due to different distributions of worker traits; and (3) changes in the distribution of worker traits within colonies due to colony-level selection. The role of genetics in this evolutionary process, unknown to Darwin, has still received little attention[2,3]. Calderone and Page[4] recently demonstrated differences in the pollen-collecting behaviour of honey bees from two artificially selected strains[5] co-fostered in wild-type colonies to be a consequence of genotypic differences between workers. These differences were caused by an artificial selection process analogous to that proposed by Darwin. Their study established a foundation for understanding genetic mechanisms underlying the evolution of division of labour but did not demonstrate a genetic basis for division of labour between related members of colonies, the essential element of the darwinian model. Here we report previously undescribed genetic differences in task specialization between related members of *Apis mellifera* colonies. These results, which support the first requirement of the darwinian model for the evolution of colony organisation, suggest that the genetic structure of an insect society plays a fundamental, and previously unrecognized, role in the division of labour.

Behavioural differentiation among worker honey bees is in part age-based, but there is also variation among workers in the rate of behavioural development and the degree of task specialization at a particular age[6,7]. Due to polyandry[8–10] and sperm mixing[10,11], honey-bee colonies are assemblages of subfamilies, each subfamily consisting of the offspring of the queen and one of her mates. We identified the subfamily membership of individuals performing specific tasks, with allozyme analysis[12,13]. Instrumental insemination[14] of queen honey bees was used to establish experimental colonies with electrophoretically distinguishable subfamilies.

Two types of task specialists were collected ($n = 40$): workers guarding the nest entance, and workers removing corpses. Both acts are readily identifiable according to simple, unambiguous criteria and are performed by a small subset of bees approximately the same age[15,16], enabling direct comparisons of guards and undertakers. Use of allozyme markers allowed blind behavioural observations.

Samples representing the proportion of adult workers in the colony from each subfamily ('controls') were obtained immediately after collecting task specialists. Individuals ($n = 40$) were collected randomly with respect to behaviour throughout the periphery of the hive, where bees of a similar age to guards and undertakers are normally located[17]. Age-matched controls ensured an appropriate reference group for guards and undertakers in the event of short-term fluctuations in subfamily frequencies[10,11]. Colonies were sampled twice for task specialists and controls, at 1–2 week intervals.

Our results demonstrate that worker genotype influences the probability of guarding and removing corpses. Significant differences in the genetic composition of samples of guards and control bees were detected 9 out of 10 times; 4 out of 10 times in samples of undertakers and control bees; and 5 out of 10 times in samples of guards and undertakers (Fig. 1). Binomial

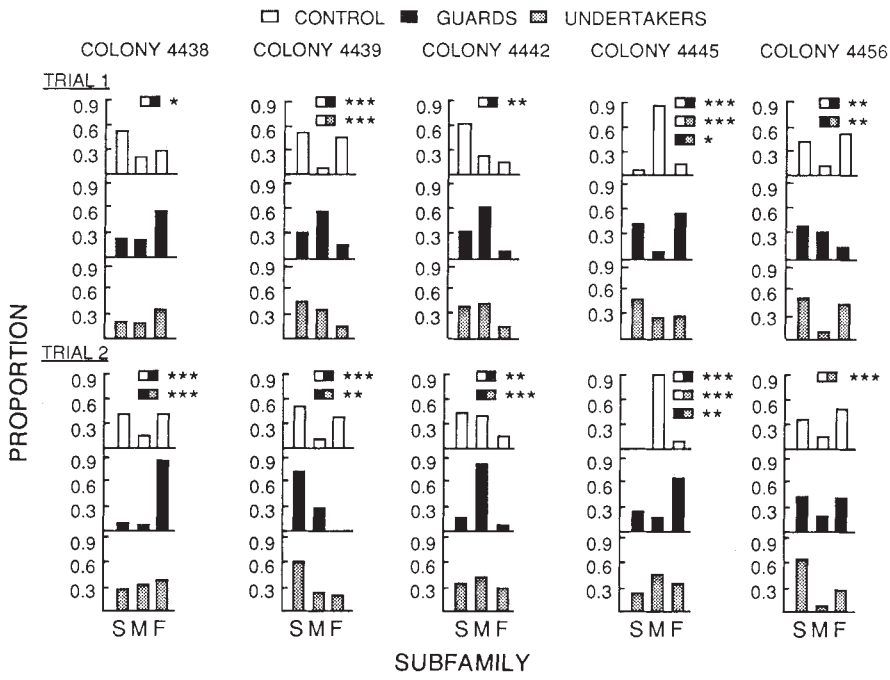

Fig. 1 Genotypic composition of samples of guards, undertakers and control workers from honey-bee colonies composed of electrophoretically distinguishable subfamilies. Statistical analyses: ◻■ = controls versus guards; ■▩ = guards versus undertakers; ◻▩ = controls versus undertakers; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$ (based on G-tests of actual frequencies). In most cases $n=40$, except: $n=39$ for Colony 4442 guards and undertakers, trial 1, Colony 4438 guards and undertakers, trials 1 and 2, Colony 4456 control, trial 2; $n=38$ for Colony 4439 undertakers, trial 1, Colony 4456 undertakers, trial 1; and $n=36$ for Colony 4456 guards, trial 1. Significant inter-trial differences for guards: Colony 4438, $P<0.02$; Colony 4439, $P<0.01$; Colony 4456, $P<0.05$; undertakers: Colony 4439, $P<0.02$.

Methods. To establish experimental colonies, an electrophoretic survey of colonies in our research apiaries was conducted; eight unrelated queens were selected as mothers of haploid drones to be used for instrumental inseminations, and three additional unrelated queens were chosen as mothers of five virgin queens. Each virgin queen was inseminated with the semen of three unrelated drones, each drone bearing a different allozyme of malate dehydrogenase, 'slow' (S), 'medium' (M), and 'fast' (F)[12]. Semen from each drone trio was pooled, diluted, and homogenized before insemination to stabilize the relative frequencies of different subfamilies over time[35,36]. Two out of five inseminated queens (Colonies 4438 and 4456) were SS homozygotes and produced worker progeny with three distinct allozyme phenotypes: SS, SM and SF. The other three colonies had SF queens that produced three subfamilies with five allozyme phenotypes: SS, SM, SF, MF and FF. Workers sampled from these colonies were grouped into three subfamilies as follows: SM and MF bees were assigned to the M subfamily because the M allele could only be paternally inherited. SF bees were assigned to the S and F subfamilies in direct proportion to the ratio of SS to FF bees in each sample, because the maternal S and F alleles segregate in a 1:1 ratio. G-tests with all five allozyme phenotype classes gave identical results to those presented.

tests indicate these differences occurred too frequently to be explained by sampling error alone ($P<0.01$, undertakers versus controls; $P<0.001$, guards versus controls and guards versus undertakers). No allozyme marker was consistently associated with low or high levels of guarding or undertaking activity (Fig. 1).

Subfamily frequencies in the control samples of trials 1 and 2 did not change significantly ($P>0.05$) for any colony (Fig. 1), suggesting that the genotypic composition of colonies was stable over the study period. Thus our results cannot be a consequence of possible age differences between control bees and task specialists coupled with age polyethism.

Inter-trial differences in the genotypic composition of guard and undertaker samples were observed in some cases (Fig. 1), suggesting environmental effects on the probability of task performance. A strong genotypic component to the observed subfamily variation is demonstrated by the persistence of specific subfamily biases for tasks from trial to trial. This was quantified by calculating the relative likelihood (RL) that a bee observed guarding or undertaking belongs to a given subfamily (i) as follows:

$$\mathrm{RL}_i = \frac{L_i}{\sum_{j=1}^{n} L_j}$$

where

$$L = \frac{\text{proportion of subfamily } i \text{ or } j \text{ in task specialist sample}}{\text{proportion of subfamily } i \text{ or } j \text{ in control sample}}$$

n = number of subfamilies in a colony

Values of RL (two per colony for each task) were analysed with an analysis of variance (ANOVA); the proportion of the variance in RL attributable to subfamily membership was 89% and 81%, for guarding and undertaking, respectively. Additional evidence for highly constant subfamily biases in corpse removal is presented in Fig. 2.

There are at least two possible explanations for our results. First, genetic differences in subfamily spatial distribution within the nest may affect the probability of encountering stimuli associated with guarding and undertaking behaviour. Possible reasons for non-random spatial distribution independent of task performance include genotypically determined temperature preferen-

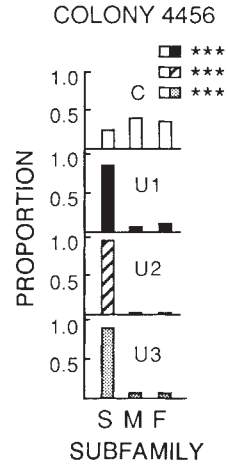

Fig. 2 Persistence of subfamily differences in task performance: genotypic composition of three samples of undertakers (U1-3) and a sample of control bees (C) collected four months after the first samples from this colony were taken (Fig. 1, Colony 4456). See Fig. 1 for explanation of statistical analyses. U1 and U2 were taken on 20 August 1987, U3 and C the next day. Bees from the S subfamily were over-represented in all undertaker samples relative to the control sample, in a pattern similar to that observed in the first trials with this colony (Fig. 1). The consistency of this effect, seen over the span of several worker lifetimes, despite differences in colony and environmental conditions associated with changing seasons, points to a strong genetic determinism for this task.

ces and kinship discrimination[18]. But in the only study on this question to date[19], members of the same subfamily were not clumped within honey-bee nests.

Alternatively, we favour the idea that a colony's subfamilies differ in task performance because they have different distributions of behavioural response thresholds for the stimuli eliciting a task. This hypothesis is consistent with previous reports of genotypic[20] and hormonally mediated[21] differences in honey-bee sensitivity to task-associated stimuli. Based on this possibility, we propose a mechanistic explanation for one of the most interesting and enigmatic forms of division of labour in the insect societies, the occurrence of individuals like guards and undertakers that perform jobs most colony members do not[22]: these individuals have rare genotypes that result in low response thresholds.

The discovery that intra-colonial genetic variation influences the organisation of labour challenges the prevailing model of highly eusocial insect colonies as superorganisms responding to environmental stimuli with behaviourally totipotent individuals[23,24]. For some tasks, particularly those involving large numbers of workers, the additive effects of all genotypes may contribute to the colony 'phenotype.' Non-additive behavioural dominance[25] effects of one or a few distinct genotypes may determine the colonial phenotype for other tasks. Negative feedback within colonies coupled with behavioural dominance may in particular affect the genetic structure of groups performing relatively rare jobs like guarding and undertaking, because the activities of a small number of bees may satisfy colony needs and maintain the stimulus level below the thresholds of less sensitive individuals. Feedback loops of task regulation may also result in less sensitive workers performing a particular task if a colony experiences a greater need for that task or lacks a subfamily with a high probability of performing it. Worker bees exhibit impressive behavioural plasticity[7], but findings of genetic variation in colony behaviour[5,26] suggest that workers do not converge on some average level of task performance in a colony, but rather express genetically determined differences. Colony behaviour is thus the product of the behaviour of its individuals, and differences between colonies are in part due to differences in the subfamily distribution of worker traits within colonies.

Our results support and extend previous findings of genetic variation in worker behaviour among different races and artificially selected strains of honey bees[26,27]. Together with those of Calderone and Page[4], they also demonstrate that genetic differences between workers are the 'grist' for the evolution of colony organisation. Heritable differences between colonies in the division of labour could also be the result of queen effects on workers[28–30], but we know of no supporting evidence.

If, in the course of evolution, worker behaviour has been under strong colony-level selection, the large amount of intra-colonial genotypic variability in task performance we observed needs to be explained. Worker heterogeneity may be an artefact of polyandry, itself selected for by factors unrelated to the organisation of work[31,32]. If this is true, it may be that colony-level selection does not reduce genetic variation because heritabilities are low due to behavioural dominance, or because fluctuations in the environment preclude the emergence of a single optimal genotype[33]. Alternatively, increased intra-colonial genetic variability may have selective value, if a collection of specialized genotypes performs more efficiently under a range of environmental conditions than a single, more generalized genotype[2,31,34]. The adaptive significance of our findings is not clear, but it is apparent that colony genetic structure affects the division of labour in at least one polyandrous insect society.

Since submitting this manuscript we have learned that Frumhoff and Baker[37] report similar results.

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A genetic component to division of labour within honey bee colonies

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Division of labour among nestmate workers is central to the colonial organization and ecological success of the eusocial Hymenoptera (ants, bees and wasps)[1]. Workers characteristically divide labour through (1) ontogenetic changes in individual behaviour[2,3] and (2) inter-individual variation in behavioural repertoire[3,4]. On the basis of current evidence, optimization models of colony demography[3,5,6] assume that variation among nestmates in behavioural repertoire arises solely through variation in environmental conditions, such as larval nutrition (inducing size-mediated behavioural differences in many ants)[3,4,7] and adult experience (effecting behavioural differences among morphologically similar nestmates)[8]. A possible genetic component to division of labour, however, has received little study[9]. Yet, the degree of genetic heterogeneity among workers within Hymenopteran colonies is often extremely high[10], a consequence of multiple mating by the queen (polyandry[11,12]) and/or the presence of multiple laying

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