

stratigraphic context and dating from 1830–1850, from excavation of a dwelling<sup>9</sup>. The sum of tetrachlorodibenzofurans (TCDFs) dominates the congener profile of archaeological peat ash, accounting for 30% of all of the dioxins and furans analysed, as in the peat-burning experiments described here (Fig. 1) and in high-chloride lignite-combustion products<sup>10</sup>. TCDF levels differed significantly ( $P=0.005$ , one-way analysis of variance) between the tested matrices in Fig. 1 (the dominant TCDF in the congener profile is a marker for peat/lignite burning).

The environmental persistence of individual congeners varies in different soils<sup>1</sup>. Dioxins undergo long-distance global transport<sup>1</sup>, and modern deposition explains the presence of dioxins in unburned peat and the high proportion of tetrachlorodibenzo-*P*-dioxin and octachlorodibenzo-*P*-dioxin congeners in these soils compared with the archaeological ash sample (Fig. 1). Even with the superimposition of modern dioxin deposition and the differential loss of

individual dioxins over time, the arable soil of Hirta still carries the signature of past peat ash, with high levels of TCDF compared with fresh peat (Fig.1). Today, 70 years after the island was evacuated, the dioxin signature accrued over centuries of peat burning is still evident, a reminder that modern humans were not the first to generate large quantities of dioxins.

**Andrew A. Meharg, Kenneth Killham**

School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK  
e-mail: a.meharg@abd.ac.uk

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Sociobiology

Worker nepotism among polygynous ants

Insect societies are a prime example of extreme cooperation, but their social life also entails the pursuit of selfish interests by society members<sup>1</sup>. Here we show that workers of the ant *Formica fusca* favour their own close kin when rearing eggs and larvae in colonies that are derived from several queens. This nepotistic behaviour indicates that ant workers are able not only to detect kin relationships, but also to pursue their selfish genetic interests if the costs to their colony are not prohibitive.

According to kin-selection theory, social insect workers should selfishly indulge their own evolutionary interests<sup>1–3</sup>. But evidence

for nepotistic kin discrimination has so far been weak or negative, and may even be precluded by informational constraints and prohibitive costs<sup>4</sup>. We therefore investigated the ability of *F. fusca* workers to discriminate between close and more-distant relatives in colonies that are headed by multiple queens (polygyny). As the workers of this species feed the queens and raise the brood, they may be in a position to manipulate brood composition if they can interpret genetic identity.

The kinship among queens in this species is  $0.40 \pm 0.14$ , and that of workers to the queens is  $0.17 \pm 0.12$  (ref. 5). If workers are more related to one of the colony queens, theory predicts that they should favour her offspring over those of the others<sup>1,6</sup>; however, if they are equally related to all of the queens, they should

have no incentive to favour the offspring of any particular one<sup>1,6</sup>.

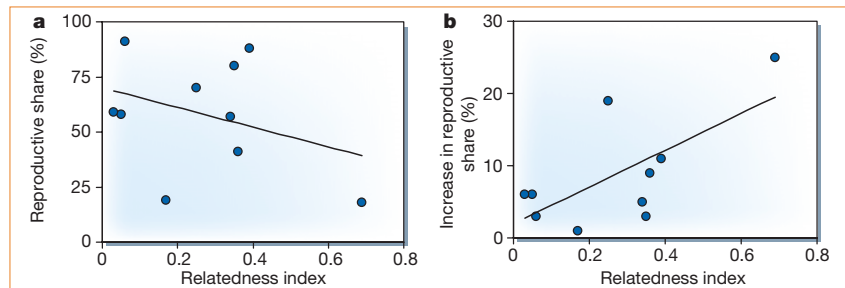
We studied ten two-queen laboratory colonies<sup>5</sup> of *F. fusca* to compare within a single cohort the reproductive apportionment at the egg and pupal stages. To determine reproductive apportionment and estimate the relatedness between workers and queens<sup>7</sup>, we genotyped at six micro-satellite loci<sup>5</sup> an average of 43 eggs, 85 pupae, both queens, and eight workers per colony. Although under laboratory conditions only the worker brood is reared, a queen's genetic representation in this brood accurately reflects her reproductive output (our unpublished results).

We found no positive association between the relatedness of workers and queens and the absolute reproductive apportionment among eggs (Fig. 1a). However, the reproductive share of the queen who was more closely related to the workers increased during brood rearing, and this change was directly proportional to the size of the relatedness difference between the workers and each of the two queens (Fig. 1b). This indicates that workers can discriminate their own kin and selectively favour a brood of closer kin. Although a difference in the viability of eggs<sup>8</sup> or the presence of diploid males<sup>9</sup> may cause a pattern of selective disappearance of eggs, neither explains the observed association between worker–queen relatedness and changes in reproductive apportionment.

We conclude that ant workers can apparently discriminate kin accurately and that they capitalize on this ability, thereby enhancing their genetic contribution to future generations<sup>1</sup>, even in the presence of several queens. Evidence of nepotism in insects apart from the honeybee (*Apis mellifera*)<sup>10</sup> has not previously been found<sup>4</sup>. This selection for the selfish pursuit of fitness is likely to be a universal feature of societies, but could be modulated by constraints imposed by a lack of accurate information or a reduction in productivity<sup>4</sup>. Power affiliations may be complex in societies in which different parties pursue their individual genetic interests.

**Minttumaaria Hannonen, Liselotte Sundström**

Department of Ecology and Systematics, University of Helsinki, PO Box 65, 00014 Helsinki, Finland  
e-mail: liselotte.sundstrom@helsinki.fi



**Figure 1** Nepotism in the ant *Formica fusca*. **a**, Absolute reproductive share during brood development among a queen's eggs as a function of her relatedness to the colony workers (correlation coefficient,  $r_s = -0.35$ ,  $n = 10$ ,  $P = 0.32$ ). **b**, Increase in a queen's reproductive share as a function of her relatedness to workers. Correlation between the two variables was highly significant ( $r_s = 0.67$ ,  $n = 10$ ,  $P = 0.01$ ; one-sided test). To exclude any other factor relating to queens' fecundity<sup>8</sup>, the change in reproductive apportionment was quantified by first regressing the reproductive apportionment of each queen among the matured brood on her apportionment among the eggs, and then using the positive residuals. The relative kin value of a queen (relatedness index) is calculated as  $r_{wq+} - r_{wq-}$ , where  $r_{wq+}$  is the relatedness of workers to the queen that increased her reproductive share, and  $r_{wq-}$  is the relatedness of workers to the queen whose share decreased.

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