

Competition for royalty in bees

SIR — Reproductive dominance is usually linked to morphological caste in honeybees, *Apis mellifera*, with the queen as the reproductive and the workers as the infertile individuals. However, in queenless colonies, workers can establish themselves as pseudoqueens, expressing all features of reproductive physiology that are otherwise typical of the morphological queen caste.

Pseudoqueens and sterile workers are completely different physiological units. In contrast to the sterile worker, the pseudoqueen has well developed ovaries, releases queen pheromones, elicits retinue behaviour, and suppresses fertility of other workers¹. Pseudoqueen behaviour is particularly well expressed in laying workers of the cape honeybee, *Apis mellifera capensis*. Within a few days after queen loss, an *A. m. capensis* worker can develop to a fully functional pseudoqueen². This physiological caste determination seems to be affected by genetic variance^{3,4}. Because the honeybee queen is highly polyandrous⁵, intracolony

genotype selection among subfamilies and individuals governs which workers are to become pseudoqueens and which remain sterile.

We studied the genotypic composition of four queenless splits of each of two *A. m. capensis* colonies over a 9-week period using single locus DNA fingerprinting⁶ (Fig. 1). Most of the patriline disappeared in the brood after dequeening, and workers of only a few patriline were able to produce offspring. Interestingly, the same subfamilies of a colony appeared to become reproductively dominant in all splits (Fig. 2). Using a sib analysis⁷ on the entire dataset, we estimated that 67% of the observed variance for reproductive dominance was due to between-family effects.

The high genetic variability of characters closely linked to fitness may seem surprising. However, a frequency-dependent selection model⁸ invoking both colony level and individual selection can plausibly explain the phenomenon. Colonies composed of dominant workers

alone are unable to produce any fertile offspring because there are no subordinate workers to attend to the brood or to rear adults. A majority of subordinate workers are required to maintain colonial homeostasis⁹, and therefore an equilibrium between subordinate and dominant types can be established.

The fitness differences between the subfamilies, however, do not necessarily require between-family competition. Direct individual fitness advantages of single workers are sufficient to explain the observed phenomena. Because only a few workers within a subfamily develop to pseudoqueens, there is also strong selection within the subfamily for reproductive dominance. Of course we cannot exclude nepotistic behaviour of the dominant patriline from our data, but it is certainly no requirement for the observed

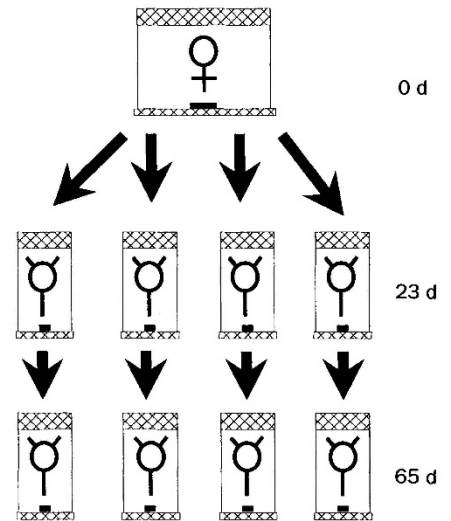


FIG. 1 Two colonies of *A. m. capensis* were dequeened and split into four equal-sized nuclei of about 4,000 bees each. Worker samples (about 40 per colony) were taken from the original colonies to determine the subfamily composition of the mother colony. After 23 and 65 days, worker brood samples (produced by laying workers) were taken from the splits. Furthermore, all queen larvae that were reared by the laying worker splits were collected. The samples were kept in ethanol until DNA processing, and were genotyped using single locus microsatellite fingerprinting as previously described^{5,6} (loci A14, A29, A76 and A107).

results, which fit well in a plain individual darwinistic fitness model.

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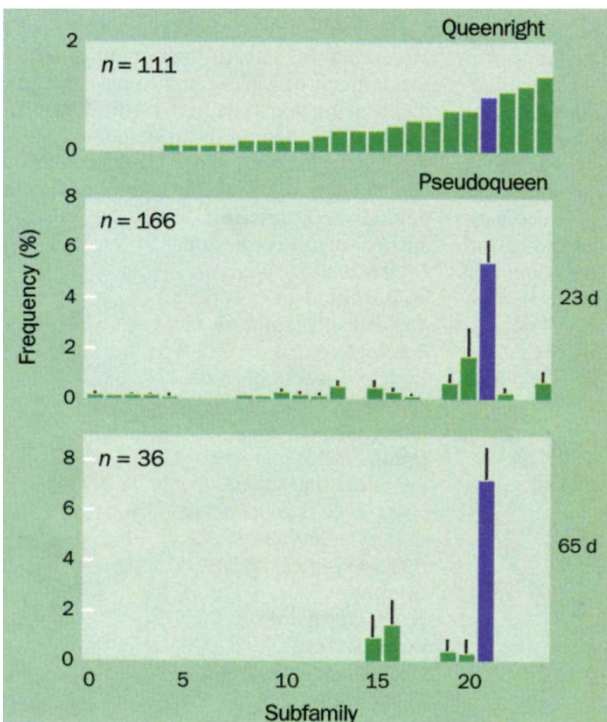


FIG. 2 Mean offspring frequencies (+ s.e.m.) of the various patriline subfamilies observed in four split units of colony A (colony B not shown) over the observational period. The number of subfamilies in the original colonies A and B were 24 and 44, respectively, indicating a very high degree of polyandry in *Apis mellifera capensis*. This figure reduced dramatically after loss of the queen. Only five subfamilies in colonies A and B were present in the brood at the end of the observation period. One subfamily in each colony was clearly dominant (purple bars) and produced 8 out of 13 reared queens. The other five queens all belonged to different patriline subfamilies.

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