

Evolutionary biology

Genetics and labour in bees

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EARLY models for the evolution of worker caste in social insects assumed that there is little genetic variation in the social unit¹. But recent genetic studies show that colonies of many species incorporate considerable variation², either because many queens are present (polygyny)³ or because the queen has mated more than once (polyandry)⁴. In this issue, Robinson and Page⁵ on page 356 and Frumhoff and Baker⁶ on page 358 demonstrate that genetic variation within bee colonies is correlated with differences in task performance. This indicates that there is a genetic basis for behavioural differences among workers, and the result has substantial implications for our understanding of the evolution of division of labour in colonies of social insects.

The two papers in this issue suggest that polyandry in the honey bee broadens the range of abilities that workers in a colony have for performing certain tasks. Robinson and Page⁵ study two behavioural patterns, guarding and undertaking (removal of corpses from the hive; see this week's cover), that are critical to colony function but are expressed by very few bees in the colony. They can distinguish worker patriline — worker offspring of different fathers but the same mother — by using electrophoretically detectable enzyme markers. Certain patrilines show a strong bias for guarding, whereas others show a strong bias for undertaking.

Frumhoff and Baker⁶ look at two behavioural patterns in which workers commonly engage during social interactions: grooming of workers by other workers and mutual feeding (trophallaxis). Cuticle-colour genetic markers (black and cordovan) distinguish patrilines in their colonies. Cordovan patrilines engage in substantially more grooming behaviour than black patrilines. There is no consistent bias in feeding behaviour; Frumhoff and Baker suggest that this difference results from the fact that some workers specialize in grooming whereas all workers engage in trophallaxis.

Crozier and Page suggested⁷, among other hypotheses for the evolution of polyandry in social insects, that a colony with high genetic variability among its workers might cope better with changing environmental conditions. Cole argues⁸, however, that polyandry is associated with large colony size, and that polyandry ensures adequate sperm supply for the production of large populations. Recently, Sherman *et al.*⁹ have proposed that the increased genetic variation in colonies resulting from polyandry might buffer the

colonies from the effects of parasites and pathogens.

The findings reported in this issue^{5,6} suggest that the high number of matings, which allow the queen to obtain sperm far in excess of the amount that can be stored or used, may have evolved as a result of selection to produce behavioural genetic variability in the worker population. But both groups of authors are careful to point out that they may have presented epiphenomena, secondary to other factors which might have led to polyandry in the honey bee.

Are queens able to select the drones they mate with to maximize the range of worker inclinations in their colony? Each of the studies in this issue used colonies whose queens were artificially inseminated from limited numbers of drones. In nature, queens mate up to 17 times¹⁰, so one next step would be to determine if these matings are non-random; that is, whether queens seek to mate with a varied sample of males.

Polygyny in social insects, particularly in ants, is common; electrophoretic studies of polygynous ants reveal low levels of relatedness (and consequently high genetic variation) among workers in such colonies³. Polyandry is less common, but is more difficult to demonstrate than

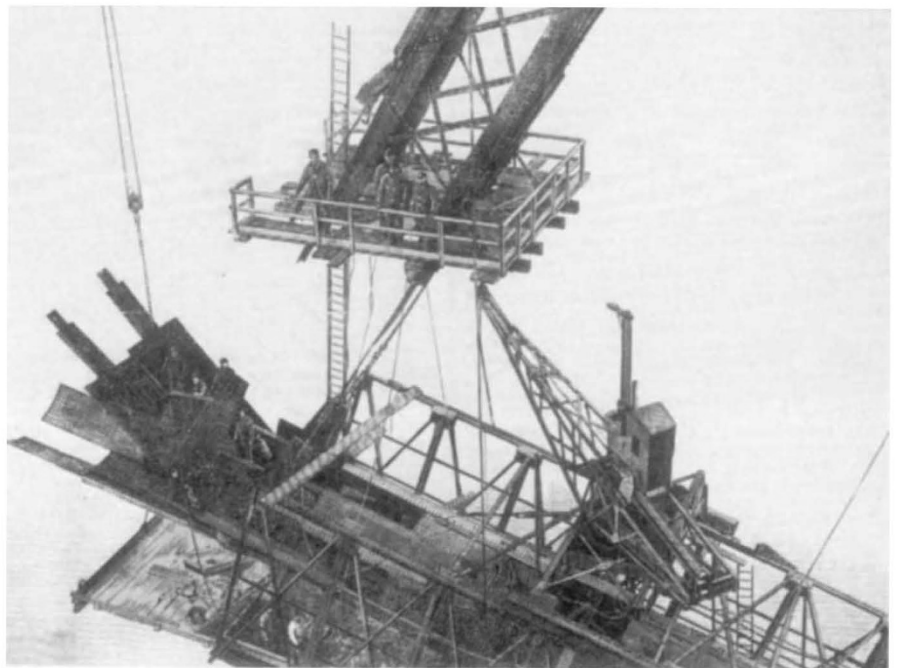
polygyny. It will be interesting if comparative studies on polygynous species reveal the same correlation between genetic background and proclivity to perform a task.

Polygyny and polyandry are usually assumed to have evolved secondarily to the presence of a worker caste. Both these mechanisms reduce genetic relatedness within colonies. Genetic models of social evolution predict that reduced relatedness should result in increased conflict of interest among workers and selection should favour reproductive capability in the workers, which are normally nonreproductive. Results such as these, which indicate continued social cooperation even as genetic variation has increased, suggest either that workers evolved in such a way that they are locked into cooperative behaviour patterns, or that we must consider models of oppression for the evolution of worker sterility¹¹. □

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We have been enabled, through the kindness of Mr. Baker, to reproduce one of the photographs of the Forth Bridge, showing the successful completion of the lower portion of the first bay. The junction we have illustrated is the connection of the web of a lattice girder with one of its booms, but here the junction alone weighs as much as an ordinary iron railway bridge of 100 feet span.