

EVOLUTIONARY BIOLOGY

Males from Mars

David Queller

In an ant species — or is it two species? — females are produced only by females and males only by males. Explanations of this revelation have to invoke some decidedly offbeat patterns of natural selection.

That men and women sometimes seem like different species is the stock in trade of pop psychologists and relationship gurus. Some go even farther: men are from Mars and women are from Venus. But in reality, human sexual differences are rather small. Even a naturalist freshly arrived from Mars or Venus would have little trouble binning specimens of men with women, and not with female chimpanzees or gorillas. There are species where males and females are different enough to have fooled real earthly naturalists. But no population geneticist would be misled — males and females mix their genes in their progeny, and as a result male and female genes comprise a common, well-mixed pool. A fascinating exception to this rule is described by Fournier *et al.* (page 1230 of this issue)¹. Males and females each reproduce clonally and, like independent species, follow separate evolutionary branches.

The surprise comes from the little fire ant, *Wasmannia auropunctata*, which is hardly obscure. An invasive pest in tropical habitats, it earns a place on a list of the 100 worst alien species². Its ancestor, like other haplodiploid social insects, must have already had two other varieties of asexuality, which together set the stage for this story. Haplodiploid species produce males asexually from unfertilized eggs (Fig. 1a), so the males are haploid — they have only one copy of each gene. Fertilized eggs become diploid females with two gene copies (Fig. 1b). In social haplodiploids, environmental differences usually induce females to differentiate into one of two castes (Fig. 2, overleaf) — ‘gynes’ become reproducing queens (Fig. 1c), whereas workers (Fig. 1d) are not just asexual but non-reproductive; they pass on their genes only by helping to rear relatives in their colony, a process known as kin selection.

In *W. auropunctata*, genetic markers show that the new gynes produced by a colony are identical to the reproducing queens (Fig. 1e). The workers, however, continue to be produced sexually. This strategy, previously reported for another ant, appears to allow the queens to pass on more copies of their genes while retaining the benefits of genetic diversity in their worker force³. The strategy cuts out the

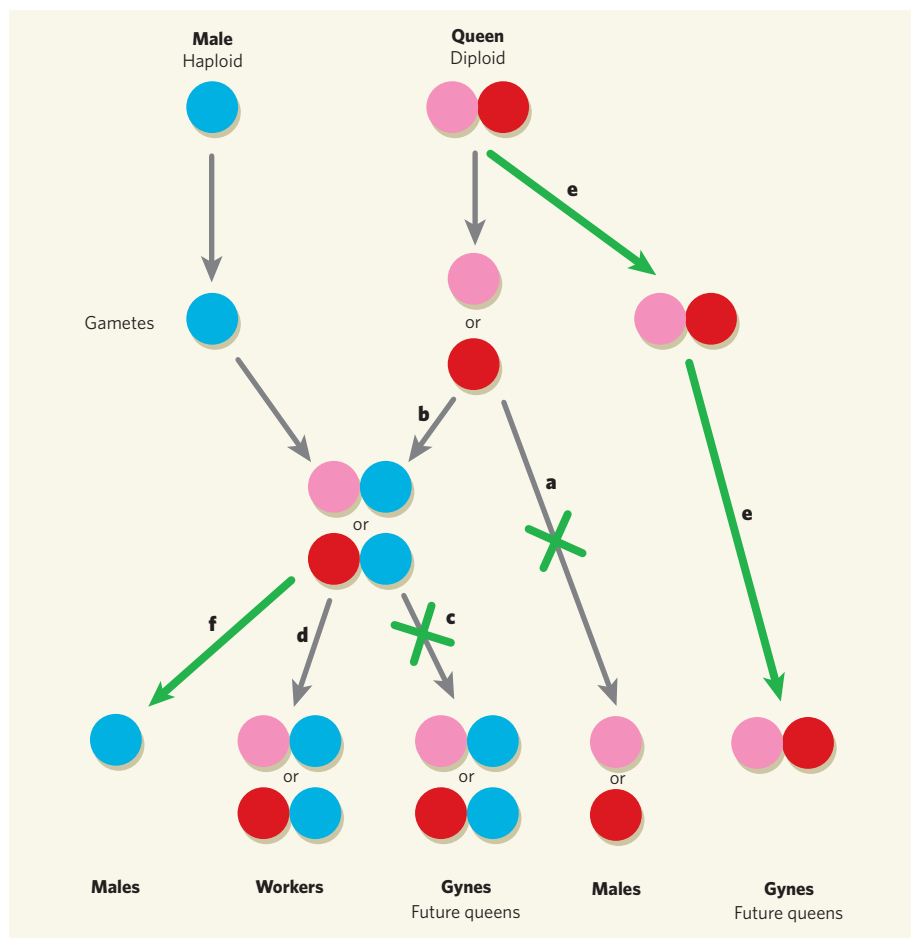


Figure 1 | Reproduction in *Wasmannia auropunctata*. Normal ants reproduce through the pathways shown by grey arrows. Each circle represents a gene (male, blue; female, red or pink). **a**, Males are produced from unfertilized eggs and therefore have one copy of each gene. **b**, Females come from fertilized eggs that can develop into either **(c)** reproductive gynes or **(d)** sterile workers. Fournier *et al.*¹ conclude that *W. auropunctata* has subtracted two pathways (green X's) and added two clonal pathways (green arrows). **e**, Gynes are genetically identical to queens, whereas **(f)** males effectively come from other males, probably by eliminating the maternal genome. The only old pathway remaining is the sexual production of sterile workers.

males as evolutionary actors — they would sire only sterile workers — but in *W. auropunctata*, the males have struck back by clonally producing other males. Fournier *et al.*¹ genotyped the sperm in the sperm storage organs of queens and found that the sperm genotype exactly matches the genotype of the males produced. They suggest that this probably results from

the paternal genome eliminating the maternal genome after fertilization, converting the diploid offspring to a haploid that will develop as a male (Fig. 1f). In *W. auropunctata*, the males seem weird enough to be from Mars.

The result is separate female and male lines that, although they combine genes in workers, never exchange them. Consistent with this, the



Figure 2 | Female castes. Two queens of *Wasmannia auropunctata*, along with workers attending to a brood. Queens and males are produced clonally, the sterile workers by sexual reproduction.

two sexes sort out into distinct branches of a genetic tree. They remain affiliated not by gene exchange but by the odd parasitic exploitation of females by males and by the mutualistic production of workers.

It is interesting to consider how this bizarre separation may rewrite the rules of colony evolution. Normally, workers evolve through kin selection based on their expected relatedness to the gynes and males they raise^{4,5}. In *W. auropunctata*, a worker's maternally derived genes — call them matrigenes (red or pink in Fig. 1) — are related to gynes but not to males. Conversely, their paternally derived patrigenes (blue in Fig. 1) are related to males but not gynes. Normally, such asymmetries are averaged out by kin selection, because worker genes can't tell when they are matrigenes and when they are patrigenes (with the possible exception of so-called imprinted genes, which have been labelled by parents, for example by tagging them with methyl groups^{6,7}).

But in *W. auropunctata*, matrigenes always remain matrigenes, so they will be consistently selected to favour gynes at the expense of unrelated males. Similarly, patrigenes remain patrigenes, and selection on them should favour related males over unrelated gynes. The result could be fierce conflict within worker genomes. Such conflict might be reduced if gynes can mate only with males of their own colony, because harming a colony's males would also harm its gynes, and vice versa.

Strange patterns of natural selection might also explain why two standard modes of reproduction have shut down. First, why would queens give up producing males by the normal pathway (Fig. 1a)? As the system stands, there is no selection for queens to produce males. A queen who produced males gains no

advantage in her own (female) gene pool; it is like putting her genes in another species. I suspect that similar logic applied, although with less force, when the female and male pools were only partially separated. The lower value of putting genes in the male pool would select against females doing so.

FLUID DYNAMICS

Impact on Everest

David Quéré

When a drop of liquid plummets onto a surface, the result is a splash — but not it seems if the process occurs at reduced atmospheric pressure. Here, perhaps, is a way to tune splash behaviour for practical ends.

A drop of liquid surrounded by air — is there anything left to discover in such a simple system, 200 years after Thomas Young and Pierre-Simon de Laplace laid the scientific foundations of capillary action? Writing in *Physical Review Letters*, Xu, Zhang and Nagel¹ reveal that air, which has been viewed as a passive fluid in the story, plays an unexpectedly active role in creating the splash that occurs when the drop hits a solid surface.

The first drops of heavy rain hitting a pond or a puddle encapsulate the full complexity of liquid–liquid impact. Hemispherical 'storm bubbles' ('frozen' by the presence of surfactants that are always present in such open environments) are distinctive features produced by the ejection of thin sheets of liquid after the shock of impact. Pioneers of high-speed imaging, such as Harold Edgerton, confirmed

Why sexually produced females cease becoming gynes may be understood by a combination of the last two arguments. First, we need to consider the patrigenes and matrigenes separately. Worker matrigenes would not gain from replacing gynes who have a copy of the gene. The patrigene would seemingly gain, but only in the female pool. Again, it is like putting copies of its genes in another species.

If further work confirms that males and females never exchange genes and follow completely different evolutionary branches, then perhaps we really should classify them as separate species. If the females remain *Wasmannia auropunctata*, we would need a new name for the first all-male species weird enough to be from another planet. *Wasmannia mars* would serve nicely. ■

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