attributable to metallic gold but which does not colour the glass; this probably represents large particles of bulk metallic gold that did not dissolve in the melt. The annealed lead-free glasses still contain minor amounts of monovalent gold because of incomplete precipitation. It has been proposed that the gold is first reduced to individual Au^0 atoms and then precipitates by nucleation and growth[11], but our spectra show no feature that could be attributed to individual Au^0 atoms, although this may be because only the quenched and largely precipitated states have been studied so far.

The presence of monovalent gold in quenched samples obtained from both $HAuCl_4{\cdot}xH_2O$ and $KAu(CN)_2$ shows that the oxidation state of the gold in the glass does not depend on the oxidation state of the gold in the starting material. Remelting of a coloured, annealed specimen of glass 2 at 1,400 °C and subsequent quenching again produced a colourless glass, whose Mössbauer spectrum showed that the metallic gold had transformed back to Au(I). This shows that the transformation of Au(I) to metallic gold is reversible and that monovalent gold is stabilized by the glass matrix.

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Social insects

Facultative worker policing in a wasp

Kin-selection theory predicts that in social-insect colonies where the queen has mated multiple times, the workers will enforce cooperation by policing each other's reproduction[1–4]. We have discovered a species, the wasp *Dolichovespula saxonica*, in which some queens mate once and others mate many times, and in which workers frequently attempt reproduction, allowing this prediction to be tested directly. We find that multiple mating by the queen leads to mutual policing by workers, whereas single mating does not.

Figure 1 Worker egg-laying in *Dolichovespula saxonica*. Workers police other workers' reproduction more in colonies where the queen has mated multiple times than in those where she has mated only once.

Workers in most species of social Hymenoptera (bees, ants and wasps) cannot mate but can produce unfertilized, male eggs. Workers and the queen therefore compete over male production. If the queen mates only once, workers are more closely related to the sons of other workers ($r=0.375$) than to those of their mother queen ($r=0.25$) and, in conflict with the queen, should prefer to rear other workers' sons. But if the queen mates multiple times, workers are more related to the queen's sons than to other workers' sons. This is expected to lead to worker policing, where workers attempt to stop each other from reproducing[1–3].

Mutual policing by egg eating occurs in the honeybee *Apis mellifera*[5] and in the common wasp *Vespula vulgaris* (K.R.F and F.L.W.R., manuscript submitted), whose queens are multiply mated, but not in the stingless bees[6] and bumblebees[7], whose queens typically mate only once. A direct within-species test is critical, however, because these taxa differ in many ways apart from kinship and, with only a few independent data points, the trend is not statistically significant.

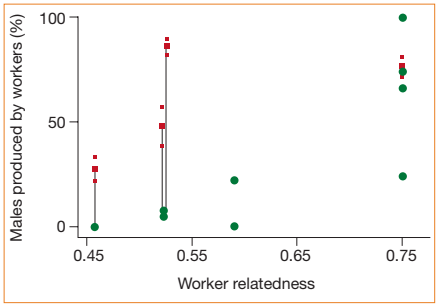

Figure 2 Pedigree relatedness among workers versus adult male production by workers in nine colonies of the wasp *Dolichovespula saxonica* (green circles). Estimates of the percentage of the male eggs that are laid by workers in four of the colonies are also shown (red squares). Nests were collected from the New Forest, UK, in 1999. Pedigree relatedness was estimated by inspection of 20 worker genotypes from each nest at three DNA microsatellite loci (Rufa 5, 13, 18)[8] to determine the number of fathers and their relative paternity. Male production by workers was estimated by genotyping 17–30 males from each nest at all informative loci. The percentage of worker-produced adult males detected for each nest was adjusted according to the probability of detecting workers' sons $\Sigma_i^n p_i(1\text{-}0.5^{l_i})$, where n is the number of patrilines in the nest, p_i is the proportional representation of the ith patriline and l_i is the number of informative loci[9] analysed at the ith patriline. This calculates the probability that a worker-produced male will inherit an allele from the queen's mate, thereby making him distinguishable from the queen's sons. The percentage of male eggs laid by workers is based on 80 h observation of four free-flying nests housed in glass-sided boxes at the Institute of Terrestrial Ecology, Furzebrook, Dorset, UK (101 queen-laid and 164 worker-laid eggs in total). Because the precise sex ratio of queen-laid eggs is unknown, three points (red squares) corresponding to a range of estimates, 2M:1F (bottom), 1M:1F (middle) and 1M:2F (top), are shown. The first produces the lowest estimate of worker reproduction and is highly conservative as *Dolichovespula* rear about twice as many females as males so that the queen probably lays more female eggs than male. The estimates of the percentage of male eggs laid by workers for the singly mated colony ($r=0.75$) lie on top of the corresponding adult male production data.

In the vespine wasp *Dolichovespula saxonica* (Fig. 1), the single queen may be either singly or multiply mated, leading to societies that differ only in kinship. We used DNA microsatellites[8] to analyse worker relatedness and male production in nine colonies.

There was a strong positive correlation between worker relatedness and male production by workers (Fig. 2; Spearman's rank correlation, $P<0.004$). Observation revealed that this was caused not by differences in worker laying — workers in colonies with singly and multiply mated queens laid nearly identical proportions of male eggs (χ^2, $P>0.86$, for all three estimates of queen-laid sex ratio) — but by removal of worker-laid eggs in the nests with multiply mated queens. In the observation colonies, worker egg production was significantly different from adult male production in the colonies of multiply mated queens (χ^2, $P<0.001$), but not in those of singly mated queens (χ^2, $P>0.39$, for all

three estimates of queen-laid sex ratio) (Fig. 2). All eight nests sampled contained reproductive workers, with 1–4 of the 20 workers examined in each nest possessing full-size eggs, also indicating that the amount of worker laying is comparable in all colonies. Interestingly, the relatedness at which policing occurs is slightly higher than that predicted from relatedness alone, suggesting that costs associated with worker male production might also favour worker policing[2].

To our knowledge, our results are the first direct evidence that multiple mating of queens causes mutual policing by workers. Policing favours workers' cooperation by preventing their reproduction[2–4], but as not all *D. saxonica* colonies have policing, here it is only partially effective in countering worker reproduction. Worker policing and cooperation have progressed further in the honeybee *Apis mellifera*, which has policing in all colonies, negligible worker reproduction and large colonies[5]. *D. saxonica* may represent an intermediate stage in the evolution of enforced cooperation. By discouraging policing in some colonies, the close kinship caused by single mating of the queen may paradoxically retard social evolution in this species and others like it.

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Embryonic development

Maternal effect of *Hsf1* on reproductive success

A protein known as heat-shock factor-1 (HSF1) is a major transactivator of stress-inducible genes in response to environmental changes, but it is also implicated in extra-embryonic development and female fertility in mice[1,2]. Here we show that mouse embryos whose mothers lack this protein are unable to develop properly beyond the zygotic stage, although oocytes were ovulated and fertilized normally. Wild-type spermatozoa do not save zygotes from lethality, indicating that the reproductive failure of females deficient in this factor is caused by a 'maternal effect' mutation[3], and that HSF1 from the mother normally controls early post-fertilization development.

Female mice lacking the gene encoding HSF1 ($Hsf1^{-/-}$ females) have normal ovaries and reproductive tracts, indicating that folliculogenesis and oogenesis do not require HSF1 expression, by contrast with the *Drosophila Hsf* mutation[4] and others affecting fertility in mammals[5]. Ovulated eggs of $Hsf1^{-/-}$ females remain properly arrested at metaphase II until fertilization, after which zygotes form with two pronuclei and a second polar body (Fig. 1a). Although mutant embryos produced by $Hsf1^{-/-}$ females can initiate early development, they do not survive after transplantation into the oviduct of *Hsf1* wild-type mice, indicating that the causes of $Hsf1^{-/-}$ infertility are intrinsic rather than extrinsic (see http://cardiology.swmed.edu/maternalhsf1/default.htm).

To determine at which stage development breaks down, we analysed the cleavage efficiency of preimplantation embryos produced by $Hsf1^{-/-}$ females, using $Hsf1^{+/-}$ females as controls, mated with either wild-type or homozygous males (Fig. 1a–d). The percentage of blastocysts at 3.5 days post-coitum (d.p.c.) was the same and independent of the genotype of the father (92.5 versus 91%, respectively; Fig. 1i).

In contrast, the embryos of homozygous females mated with either $Hsf1^{+/+}$ or $Hsf1^{-/-}$ males were blocked mainly at the 1-cell stage and development at 3.5 d.p.c. was poor (Fig. 1j). Unlike the embryos produced by heterozygous females, none of these mutant embryos reached the blastocyst stage at the appropriate time, and only 6 of 33 (18%) embryos from the $Hsf1^{-/-} \times Hsf1^{-/-}$ intercross reached the 2-cell stage. A significantly higher fraction of those sired by $Hsf1^{+/+}$ males progressed beyond the 1-cell division (20/34; 58%) ($P < 0.001$), but the difference does not persist beyond this stage (Fig. 1j). Our findings show that the survival of the offspring is determined mainly by the maternal genotype, and that $Hsf1^{-/-}$ is therefore a maternal-effect mutation[3].

Embryos might die at the 1–2-cell stage because of a failure to initiate the zygotic transcriptional activity required to complete the transition from maternal to embryonic control of development[6]. As spontaneous expression of Hsp70.1 indicates the onset of transcriptional activity at the late 1-cell stage[7–9], we used Hsp70.1-Luc transgenic lines, in which a luciferase reporter gene is driven by the murine Hsp70.1 promoter[8], to test this idea directly. At 1.5 d.p.c., embryos from $Hsf1^{+/-}$ and $Hsf1^{-/-}$ females that had been mated with

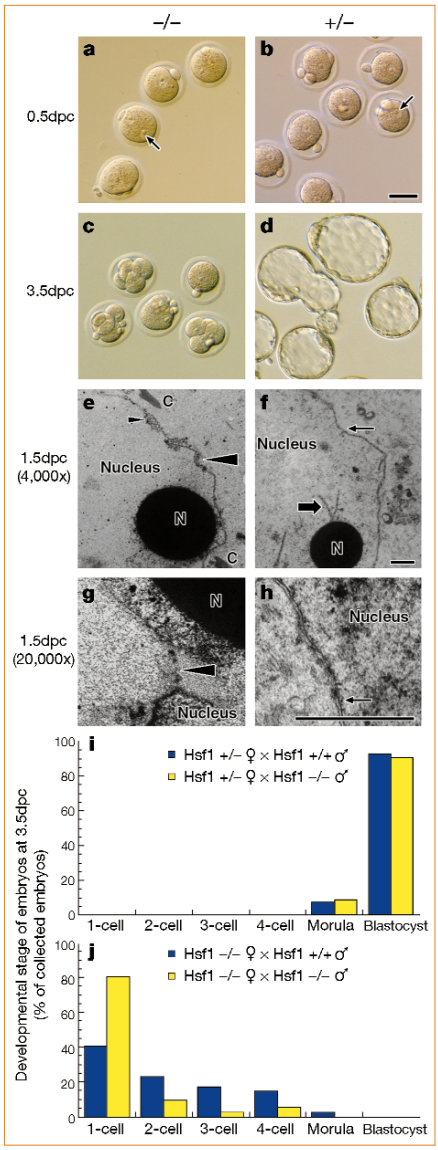

Figure 1 Developmental fates of preimplantation embryos collected from $Hsf1^{-/-}$ and $Hsf1^{+/-}$ females. **a, b,** One-cell embryos have similar pronucleus-like structures (arrows) at 0.5 d.p.c. **c, d,** At 3.5 d.p.c., when almost all embryos from matings between $Hsf1^{+/-}$ females and either $Hsf1^{+/+}$ or $Hsf1^{-/-}$ males produce blastocysts, those from $Hsf1^{-/-}$ females are blocked or unequally cleaved. Scale bar, 50 μm. **e–h,** Reduced survival of mutant embryos corresponds with ultrastructural abnormalities in 2-cell embryos: heterochromatin (small arrowhead in **e**), non-specific crystalloids ('C' in **e**), absence of intranuclear membrane disruption in nuclear membranes (arrowheads in **e** and **g** versus small arrows in **f** and **h**). Scale bars, 1 μm; N, nucleolus. **i, j,** Developmental profiles for $Hsf1^{+/-}$ (**i**) and $Hsf1^{-/-}$ (**j**) females.

$Hsf1^{+/+}$ transgenic males both showed luciferase activity significantly above the background level (50 ± 0.5 ALUs versus 41 ± 0.4 ALUs, respectively) (http://cardiology.swmed.edu/maternalhsf1/default.htm). The *Hsf1*-mutant zygotes therefore apparently express heat-shock proteins, showing that zygotic transcriptional activity can begin without HSF1.

Our results do not exclude the possibility that the level of transcriptional activity, or the control of the target genes to be tran-