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system. One can then ensure that the photons impinge on the mirror at just the right time in the system's cycle to achieve a maximum damping (or amplification) effect — rather as a hand on a child's swing at the right time in the cycle increases or decreases its amplitude of oscillation.

With tiny mirrors, this kind of control is far from trivial. Gigan *et al.*[2] and Arcizet *et al.*[3] achieve it by constructing a mirror that forms one end of a very high-quality optical cavity and functions as plunger, mass and spring all in one. Kleckner and Bouwmeester[4], by contrast, use the cavity only for 'reading out' the position of the fluctuating flexible mirror through precise measurements of the transmitted and reflected light-intensity profiles. The position parameter is then fed with a delay into an electronic feedback loop that controls the intensity of a second laser beam separate from the source of the cavity photons. This beam impinges directly on the mirror[7]. Such a configuration mimics the function of the plunger, but the precise timing of the second beam that thus becomes possible provides a tremendous amplification to the damping, and hence a record optical quiescence effect.

In all these experiments[2–4], the degree of cooling achieved so far is limited by the heating that results from vibrations of the mirror's flexible attachments, and most probably from residual optical absorption by the mirror. To observe the promised quantum-mechanical effects, cooling to just a few millikelvin is needed. That could require the use of microfabrication techniques to produce mechanical oscillators of lower mass that are more easily damped, and cavities of increased optical quality.

Among the prizes for such endeavours could be the chance to study quantum superpositions of a photon and a macroscopic mechanical oscillator. That in turn might find practical use in ultra-precise methods for displacement sensing and for measuring the mass of single atoms and molecules. The road to that destination is a long one; but it is at least now well signposted. ■

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EVOLUTIONARY BIOLOGY

To work or not to work

David C. Queller

Coercion, not kinship, often determines who acts altruistically in an insect colony. But underlying affinities for kin emerge when coercion is removed: kin selection is what turns suppressed individuals into altruists.

When Shakespeare's Prince Hamlet remarked that his uncle Claudius was "A little more than kin…" he was referring to the added relationship of stepfather that came after Claudius killed Hamlet's father and married his mother. "A little more than kin" could also describe a feature of many social insects. Owing to their odd genetic system, called haplodiploidy, full sisters in ants, bees and wasps are related by 3/4, more than a little above the standard value of 1/2. Historically, this extra kinship figured prominently in the acceptance of W. D. Hamilton's theory of kin selection[1], which holds that workers evolved to altruistically forgo reproduction because they can pass on more of their genes by raising siblings. But a series of papers[2–5], including one on page 50 of this issue[3], shows that the other half of Hamlet's description — "…and less than kind" — may be more apt. Workers are less than kind both because they must be coerced into their 'altruistic' roles and because workers are often also the ones doing the coercing.

Of course, kin selection is not just about relatedness; a little more or less kinship can matter less than larger differences in the costs and benefits of altruism[6,7]. A study of a Malaysian hover wasp by Field *et al.*[2] provides an elegant demonstration of this point. Some workers work harder than others, and relatedness to the queen does not explain the difference. In this species, rank comes with age. The second-oldest female is the heir apparent, and she reduces her risky foraging. Field and colleagues' experiments showed that this is causal. Removing the second-ranked female causes the third-ranked female to reduce her foraging in line with her improved prospects. Similarly, the amount of prospective gain also mattered; experimentally reducing colony size (adults and brood) caused second-ranked females to increase altruistic foraging, consistent with the diminished value of inheriting the queenship.

Thus, workers slacken off when they may become queens and work hard when that path is blocked. In social insects that, like the hover wasp, have small colonies and morphologically similar queens and workers, it is usually the queen that does the blocking by her dominance behaviour. For social insects with larger colonies, queen dominance is often replaced by other forms of control. First, there is nutritional coercion. Poorly fed females become small workers and well-fed ones become large queens. This limits the ability of workers to reproduce, but in most species it does not eliminate it fully. Given an opportunity, workers often will lay eggs. In a large colony, the queen could not successfully police all such behaviour and often ignores it. Instead, other workers do the policing, destroying the eggs of their co-workers[8].

A comparative study of ten policing species by Wenseleers and Ratnieks[3] again shows that altruism is modulated more by constraints on worker reproduction than by relatedness. The species with the highest fraction of fully committed altruistic workers — those that do not lay eggs — tend to be those with lower relatedness, contrary to simple expectation. Instead, more workers are fully committed when policing is most effective, as measured by the fraction of worker-laid eggs eaten by either queens or other workers. Workers are not leaping at every opportunity to be altruistic; they are coerced into that role, often by their fellow workers.

Does this mean that Hamilton's kin-selection theory is dead? The answer is no. One could invoke the efforts social insects make to exclude non-relatives from colonies, or the astonishing sex ratios that reflect kin-selected preferences for sisters over brothers[7]. But let us stick with the issue of direct reproduction. For

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Figure 1 | Queen control. A comb of the stingless bee *Melipona* with the cell caps removed to show female larvae. Each female receives the same food, and therefore can choose whether to develop as a worker (identifiable here as those with a large head and eyes) or as a queen (small head and eyes). So many females opt to become queens that the workers kill off the surplus[3], a form of control that in this species replaces queen selection through nutrition.

nine of the ten species studied[3], there are data on worker reproduction in queenless colonies where there can be no policing in favour of the queen's eggs. Two things change as a result. First, freed from policing, a higher fraction of workers opt to lay eggs. But, remarkably, many individuals still help instead of reproducing, and the fraction that help is now positively correlated with relatedness. Relatedness does matter, and this must be the reason that coercion can induce workers to help.

Wenseleers and Ratnieks[5] earlier found a similar result when nutritional coercion is absent. In honeybees and their relatives the stingless bees, most species use nutritional coercion to limit queen production to a few at a time. Few are needed, because new queens can reproduce only by usurping the mother queen, or by acquiring a colony on the rare occasions the colony splits into two. The exception is the stingless bee genus *Melipona*. Here, all brood cells are pre-provisioned equally, and then sealed. A developing larva can therefore choose for herself whether to develop as a queen, with a larger abdomen, or as a worker, with larger fore parts (Fig. 1). Many females choose to develop as queens, showing their preference in the absence of constraint. This can result in hundreds of surplus young queens in a colony, so a new level of control has evolved. The workers slaughter the excess queens, so that the nest evokes the climactic scene of Hamlet, with royal corpses littering the stage. This is a great waste, but shows that it is nutritional coercion that normally keeps queen numbers in check. Yet this case, too, reveals that coercion is not everything and relatedness is important. More than 75% of females still choose the altruistic worker role, and the proportion is higher in species with higher relatedness[5].

Finally, it should be remembered that Hamilton's kinship theory is not just about altruism *per se*, but about how all traits of altruistic workers evolve. When honeybee ancestors first evolved sociality, the workers could not waggle dance to convey information to each other, or suicidally detach their stings to better repel enemies, or police each other. These features, and all specialized features of workers, had to evolve by kin selection, through their indirect effects on relatives who could pass on genes for these traits. For example, the surprising positive correlation between relatedness and worker laying[3], which has been confirmed in a much larger comparative study[4], is expected under policing. Low relatedness among workers favours workers policing each other. Thus, although policing keeps suppressed workers from fully expressing their kin-related interests, policing is itself kin selected.

Many social conflicts create winners and losers. But only kinship allows evolution to make creative use of the social losers, turning them into reproductive police, exquisite communicators and heroic defenders. When Hamlet suffered the slings and arrows of outrageous fortune, he debated putting an end to himself. Social insect workers do sometimes choose suicide but, because of kinship, this hamiltonian choice is profoundly different from the hamletian dilemma. The stinging honeybee worker commits suicide when her sting is torn out, but this saves her kin. She is not making an escape from outrageous fortune, but making the best of it — not fearful of what dreams may come, but hopeful for what genes may come. However socially constrained her life may have been, her last action makes her own clear statement: long live the kin! ■

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GEOPHYSICS

Same old magnetism

Edward Irving

Latitudes at which ancient salt deposits occur show that Earth's magnetic field has always aligned along its rotation axis. One possible implication is that ancient global glaciations were not caused by a realignment of this axis.

In a paper of admirable scope and thoroughness that appears on page 51 of this issue[1], David Evans analyses the magnetization locked into rocks associated with salts from all over the globe that have been deposited over the past 2,500 million years. Taking as a working model the 'geocentric axial dipole' — the idea that, averaged over thousands of years, the magnetic field at Earth's surface resembles the field of a magnet, or dipole, at Earth's centre[2,3] — these magnetizations and this model provide clues to the past evolution and interplay of Earth's magnetism, climate and geography.

In the geocentric axial dipole model, the north and south poles of Earth's internal magnet are aligned along Earth's axis of rotation. This simple axial form is thought to be caused by rotational forces that guide the motions of Earth's conducting liquid core, and so constrain the average surface field. Under favourable circumstances, rocks become magnetized along the direction of the ambient geomagnetic field as they are formed. Thus, by sampling sequences of rocks with formation dates spanning several thousands of years, one can determine the past average direction of the field, the 'palaeolatitude' of the sampling locality and the position of the palaeomagnetic pole at the time. For the past 5 million years, these poles coincide with the present rotational pole; the giant dipole model has therefore been valid for at least this long.

For rocks of much earlier ages, the palaeomagnetic poles determined from rocks from different sampling sites are widely dispersed. This is the result of continental drift and seafloor spreading in the intervening period. If we restore the continents to their original positions using the geometrical methods of plate tectonics, palaeomagnetic pole positions agree very well[4]. Such corrections go back some 200 million years, and again imply that the geomagnetic field has been a geocentric dipole for that period.

But this evidence does not tell us that the field was also axial. To determine this, one first assumes that the geocentric axial dipole model holds, and determines the latitudes at which temperature-sensitive deposits were laid down from their magnetization directions, or, in the case of salts, those of similarly aged rocks. If these palaeolatitudes are compatible with the modern latitudes of similar deposits, the geocentric axial dipole model is likely to be valid.

The deposits that are the object of Evans's studies[1] are known as evaporites. They comprise beds of, among other things, gypsum, anhydrite, halite and potassium salts, and are of huge economic importance. They were formed by intense evaporation of enclosed saline lakes or sea water. The conditions for their formation must therefore have been hot and dry, as expected typically in latitudes lower than 30°. Very near the Equator, however, it is too wet for them to form.

Evans shows that, consistently over the past 2,500 million years, evaporites have been deposited predominantly between latitudes 10° and 35° (Fig. 1, overleaf). This is a beautifully documented testament to uniformitarianism — the doctrine that today's geological processes have always occurred in a broadly similar manner.

Interest in the interplay between the geomagnetic field and ancient climate zones has been spurred by evidence in a wide range of latitudes, including at sea level near the Equator,