

relatedness between group members). Clearly, high relatedness represses competition and the fitness of all group members increases. However, when relatedness is low, intense competition reduces the fitness of everyone. Hence this mechanism cannot explain cooperation when relatedness is low, for instance when different species of replicators combined in the formation of early cellular life.

A third mechanism which would permit the development and maintenance of cooperation is mutual policing within groups, as presented by Frank in his most recent work on this question<sup>3</sup>. A policing strategy is one where individuals decrease their individual competitiveness in order to contribute to a mechanism that reduces competition between all the group members and increases the fairness of distribution of resources. Frank extended the competition model described above by incorporating policing. Let  $a_{ij}$  be the contribution of the  $j$ th individual to policing ( $0 < a_{ij} < 1$ ), which costs that individual  $ca_{ij}$ , and let  $a_i$  be the average level of policing in the group. Now individual fitness is determined by

$$w_{ij} = \left[ a_i + (1 - a_i) \left( \frac{z_{ij}}{z_i} \right) - ca_{ij} \right] \times [1 - (1 - a_i)z_i] \quad (3)$$

The second square bracket describes the overall productivity of the group, which is enhanced by increasing the strength of policing (increasing  $a_i$ ). The first bracket describes the fraction of this productivity which the  $j$ th individual obtains. A fraction  $a_i$  of the resources are distributed fairly under the control of the policing policy, the remainder are allocated in terms of relative competitive ability ( $z_{ij}/z_i$ ). Finally, each individual's success is reduced by the cost of its contribution to policing:  $ca_{ij}$ . Consider a group with no policing ( $a_{ij} = a_j = 0$ ), which is at equilibrium with

each individual having competitive intensity given by eqn (2). Frank shows that a mutant which invests a small amount in policing will increase its fitness providing

$$r < 1 - c \quad (4)$$

Thus, the very interesting result is obtained that low relatedness is more conducive to the spread of policing than is high relatedness. In this simple model, if condition (4) is satisfied then subsequent selection will cause  $a$  to increase to  $a \rightarrow 1$ , and as policing increases, individuals will greatly increase their competitive intensity to cope with this.

A more realistic version of the model considers that individuals have finite resources which they can allocate to non-competitive aspects of fitness, competitive traits and policing traits. Now, allocating resources to competitive or policing traits can only be achieved by reducing allocation to noncompetitive aspects of fitness. This prevents the runaway in competitive intensity, and both  $a$  and  $z$  settle at intermediate values.

More interestingly still, this model predicts that if individuals differ in size of their intrinsic resources, then they will all invest the same in competitiveness, but will invest different amounts in policing. Small differences in resource levels often lead to large differences in allocation to policing, with stronger individuals investing a larger proportion of their resources than weaker individuals. Frank draws a parallel between this result and the conclusion of Clutton-Brock and Parker<sup>5</sup> – that in animal social groups, weaker individuals that might be tempted to disrupt group cohesion are held in check by the threat of punishment by dominant individuals.

Policing is an intuitively appealing cooperation-sustaining mechanism. It does not require assumptions of memory, strategy and mixing (unlike game theory arguments), nor does it require relatedness between individuals (unlike kin selection).

Indeed, it is even more effective when individuals are unrelated. The pioneering work of Frank suggests that simple assumptions about the form which policing takes can lead to clear and interesting predictions about the costs and benefits of cooperation and group formation. However, as Frank's models are simple, they necessarily make restrictive assumptions about the form which competition takes, the way in which competitiveness within a group affects the performance of the group, and the way in which an individual's allocation of resources affects different aspects of its fitness. However, we hope that the interesting results that he has already obtained and the potential applicability of policing to many cooperative situations will induce others to develop the theory further, and explore the robustness of the general predictions given here.

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lower likelihood of paternity; time or energy costs; and predation risks associated with seeking out additional mates.

In species without material benefits from female promiscuity, the optimal strategy would seem to be careful mate assessment and copulation with the single best male encountered. However, molecular paternity studies and behavioural data contradict this viewpoint, because in many species, females copulate with several males within a single reproductive cycle<sup>1</sup>. Researchers have therefore asked whether female promiscuity is maintained by indirect 'genetic' benefits arising from the production of superior offspring. We

## Female promiscuity and genetic incompatibility

Accounting for female promiscuity has always challenged behavioural ecologists. What advantage can females derive from mating with more than one male in a single reproductive cycle<sup>1,2</sup>? One widely accepted explanation is that direct 'material' benefits increase female fecundity or longevity. For example, during copulation males may donate nutrients that

allow greater egg production; or remating may ensure an adequate supply of sperm for fertilization. In many species, though, there is little evidence for direct benefits. In contrast, having numerous sexual partners always carries costs. These include the risk of acquiring sexually transmitted diseases; a reduction in parental care by male breeding partners because of their

**Box 1. The natural history of *Cordylohermes scorioides***

Individuals inhabit the ephemeral microhabitat under the bark of decaying trees from two plant families (Moraceae and Apocynaceae). This habitat only becomes available when a tree is newly fallen or dying. Harlequin beetles (*Acrocinus longimanus*) are attracted to just such trees for the purpose of mating and egg-laying, and the pseudoscorpions exploit this practice by hitching lifts under beetles' wing covers to reach their prime habitat. Beetles are only attracted to recently dead trees, however, so pseudoscorpions that disembark eventually become marooned.

Several generations then pass until growing beetle larvae have developed into adults. When these beetles disperse, pseudoscorpions can again catch a 'maiden flight' to another decaying tree. Not all pseudoscorpions get to disperse though, as there is limited space under beetles' wings. Because females are sexually receptive on both trees and beetles, there is intense male-male competition to monopolize the limited space on beetles. Larger males tend to win these interactions, which could potentially create recurring genetic bottlenecks every few generations favouring larger males. Sperm storage from tree matings reduces this large-male mating advantage, however, with 86% of females that board beetles having already mated<sup>8</sup>.

Earlier work also showed that last-male sperm precedence (often seen in two-male mating studies with insects in the laboratory), which would benefit the larger males on beetles, breaks down when females are allowed to mate with more than two males.

already know that females mated to attractive males bearing larger sexual ornaments sometimes produce more viable offspring, demonstrating that females can choose males with 'viability genes' ('good genes')<sup>3</sup>. But how is this reconciled with multiple mating by females?

At first glance the two phenomena are contradictory. The existence of heritable variation in viability suggests females should only mate with the best male. One solution, strongly supported by work on birds, is that social constraints sometimes prevent females from raising young with the males they would like to sire their offspring. Females may therefore pair with one male to obtain parental assistance, but perform extra-pair copulations with a highly ornamented male to produce more viable offspring<sup>4</sup>. More generally, when time is limited, females may initially mate simply to ensure an adequate supply of sperm, but remate if they subsequently encounter a better quality male. This kind of multiple mating is a far cry from genuine promiscuity though. Presumably, females carefully assess prospective partners before remating.

Although sperm 'trade-in' explanations may account for remating by birds, in many other taxa the situation is closer to true promiscuity. Females mate with numerous males, seemingly to ensure a supply of sperm from several males, rather than to improve on a previous choice of partner. What genetic benefits could accrue from this behaviour? One general answer came from work on the European adder (*Vipera berus*)<sup>5</sup> and green lizard (*Lacerta agilis*)<sup>6</sup> where multiple mating raised offspring fitness. In adders, multiply-mated females produced fewer stillborn offspring than singly-mated females. In green lizards, the more sexual partners a female had, the greater her egg-hatching success, the lower the number of offspring born with physical defects, and the greater juvenile survivorship. Unfortunately, both studies were correlational and the spectre of a spurious association, although improbable, could not be eliminated. Nevertheless, it was argued that these findings are best explained if males with superior 'viability genes' produce sperm that outcompetes that of other males. Neither study provided a proximate mechanism,

but the simplest explanation was that higher-quality males produce more, rather than better, sperm, thereby winning in lottery-like sperm competition.

Both studies also raised a puzzling question: why can't females recognize and mate with genetically superior males in the first place, thereby avoiding any costs of promiscuity? One answer put forward, at least for lizards, was that traits reliably signalling male genetic quality may not exist<sup>7</sup>. Hence, a female's only option is to mate promiscuously and allow sperm competition to filter out weaker males' sperm. Until recently, the story could thus be summarized as follows: when reliable cues to intrinsic male genetic quality are lacking, females mate promiscuously to generate male-male sperm competition which is won by sperm of higher-quality males.

In a new set of papers<sup>8-11</sup>, Jeanne and David Zeh propose an alternative explanation. Their conclusions are based on molecular work, some deceptively simple experiments, and detailed knowledge of the fascinating natural history of the tiny, neotropical pseudoscorpion, *Cordylohermes scorioides* (Box 1). Using DNA fingerprinting with single-locus minisatellite probes, the Zehs uncovered widespread multiple paternity in *C. scorioides*. A conservative estimate was an average of two sires per brood, with at least 17% having three or more sires<sup>8</sup>. Laboratory experiments further showed that females actively choose to be inseminated by more than one male. Virgin females invariably picked up the first sperm packet a male deposited, but 88% then refused the next sperm packet he produced. When placed with a new male shortly afterwards, however, females again picked up the first sperm packet deposited but refused subsequent packets. Detailed behavioural observations confirmed that acceptance of a sperm packet requires the cooperation of the female. Multiple paternity will therefore only arise when females actively choose to mate with several males<sup>9</sup>.

The next experiment compared the reproductive output of females mated singly or multiply<sup>9</sup>. Comparisons were made between naturally-mated females collected in French Guiana, Panama and Trinidad, and females mated to either 2-3 males or a single male in the laboratory. There was no difference in the number of nymphs hatching from field-mated females and females that mated multiply in the laboratory, but the number was significantly lower for singly-mated laboratory females (51.5 versus 37.7 nymphs). The main cause of this difference in output was complete brood failure by 27% of singly-mated females compared to 8% of multiply-mated females; but even when failed broods were excluded, singly-mated females still produced fewer nymphs.

**Box 2. Genetic conflicts and incompatibility**

Some males' gametes are more likely than others to produce viable zygotes when they fertilize a given female's egg. A simple illustration of this comes from inbreeding depression<sup>12</sup>. Growing evidence for intra-genomic conflict suggests that gametic incompatibility may be widespread. 'There is a genetic conflict if the spread of one gene creates the context for the spread of another gene, expressed in the same individual, and having the opposite effect'<sup>15</sup>. So-called selfish genetic elements promote their own over-representation in the next generation relative to other alleles at the same loci. Usually this is at some cost to the individual (genome) bearing the selfish element. This sets the stage for the evolution of suppressor genes that act to neutralize the selfish element.

Examples of selfish genetic elements include meiotic drive, maternal effect lethals and genomically imprinted genes; and endocellular symbionts that feminize, sterilize or kill males. Costs to individuals (and unlinked genes) come in the forms of reduced gamete production, overproduction of the more common sex and lower reproductive output. Details vary depending on the exact mechanisms involved, but it is generally true that the costs of selfish elements vary depending on whether an individual is homozygous or heterozygous for the element, and whether or not an individual also carries suppressor genes. Hence, expected survival or viability of progeny depends on the genetic make-up of potential mating partners with respect to selfish genes and suppressors. Some mating combinations may produce normal progeny, while others may lead to the production of fewer, less viable or sterile progeny (for a detailed review see Ref. 15).

The results at this stage, like those for green lizards, were consistent with preferential fertilization by males with superior 'viability genes', but a final experiment refuted this explanation. Each of 67 males was mated to two virgin females. If multiple mating is beneficial because sperm competition is won by males with intrinsically 'good genes' for viability, females mated to the same male should show similar reproductive success. They did not. The number of nymphs produced by females mated to the same male showed absolutely no correlation, even when data were corrected for female body size. There were 29 cases of brood failure, but this occurred in both females for only two of 67 males. The most plausible source of brood failure was genetic incompatibility. Because multiple mating improved female reproductive success, it therefore follows that post-copulatory mechanisms must exist whereby each female can bias fertilization towards sperm from genetically compatible males.

The Zehs suggest that these findings provide a broad-based explanation for female promiscuity. In a review of the recent explosion of literature on genetic conflicts<sup>10</sup>, they present a list of phenomena that can lead to inviable or inferior offspring because sexual partners are genetically incompatible (Box 2). They then argue that it is easier for females to choose genetically compatible sperm using post-copulatory mechanisms rather than pre-copulatory mate choice<sup>11</sup>. After all, with a few exceptions<sup>12</sup>, it is probably difficult for a male reliably to signal, and a female to detect, that he carries specific genes. Following copulation, however, cellular and molecular interactions may allow for direct assessment of genetic compatibility. In addition, in viviparous species, females may be able to overproduce zygotes and then reallocate resources from defective to more viable offspring.

The biggest challenge for the credibility of the Zehs' claim is to accumulate convincing evidence that females use post-

copulatory processes to bias fertilization towards genetically compatible sperm. Traditionally, the emphasis in multiple-mating studies has been on male-male sperm competition rather than female sperm selection or other types of 'cryptic female choice'<sup>2</sup>. Ironically, evidence for a female-mediated process that reduces the risk of genetic incompatibility in offspring comes from new work on green lizards. Controlled matings show that physical deformities are common when closely related lizards breed ('inbreeding depression')<sup>13</sup>. However, the low frequency of offspring deformity for multiply-mated females implies that fewer offspring than expected are inbred. Confirmation of this came in a recent *Nature* paper by Mats Ollson and colleagues<sup>14</sup>, in which DNA fingerprinting revealed that the more fingerprint bands a male shared with a female (relative to the other males with whom she mated), the smaller the proportion of the brood he sired. Cryptic female choice therefore led to male fertilization success being dependent on his genetic similarity to the female. There is also suggestive evidence for even more refined female-sperm (actually egg-sperm) interactions. In mice, individuals heterozygous at the major histocompatibility complex (MHC) have higher fitness than homozygotes. Recent *in vitro* fertilization experiments sometimes yielded more MHC heterozygotes than expected by Mendelian inheritance<sup>12</sup>.

Determining the proximate mechanisms responsible for these post-copulatory processes of cryptic female choice remains a major challenge (a comprehensive review lists over twenty general possibilities)<sup>2</sup>. Regardless of the exact mechanisms, though, these results suggest that females can benefit from promiscuity when post-copulatory tactics reduce the risk of eggs being fertilized by genetically incompatible males<sup>10,11</sup>.

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## Landscape alteration in the Americas

In the five centuries since Europeans discovered the New World, the Americas have been dramatically modified. Land alteration has closely paralleled patterns of European colonization. In North America, colonization began on the eastern seaboard and spread progressively westward, where it continues apace today. Patterns differed in South America, where change has been greatest in accessible coastal

regions and in cooler climates in the southern half of the continent and mountains and foothills of the Andes.

Today, the Americas are being altered more rapidly and profoundly than at any point in their European history. These changes are most evident in the tropics. Throughout Central America, vast areas of forest have been cleared and fragmented in recent decades. There also has been

rampant development in the eastern and southern Amazon, and in only the past few years, an explosion of logging activity in the Guianas and central Amazon. Almost equally dramatic has been the transformation of old-growth forests from clear-cut logging in North America, especially in the Pacific Northwest and western Canada.

Since the early 1980s, scientists and policy-makers have become increasingly aware that potent natural forces link regional and global ecosystems. Large-scale deforestation in the Amazon, for example, is contributing to global warming via the greenhouse effect, and may be altering