noise, dissipation and resonances in the environment and in the structure itself. Beating these down remains a great challenge for the field. ■

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Behavioural ecology

Father knows best

Paul W. Sherman and Bryan D. Neff

When females mate with several males, paternity may be uncertain. But male savannah baboons are seldom confused: when intervening in fights between youngsters, they generally support their own offspring.

Behavioural ecology is the study of how natural selection shapes behaviour in relation to ecological and social conditions. A fundamental principle is that individuals should promote the spread of their own genes over those of competitors. For example, adults sacrifice themselves to defend and nourish offspring. But they try to avoid providing assistance to non-relatives (that is, they avoid 'misdirecting' their nepotism), usually by guarding their mate against other sexual liaisons and attempting to distinguish their own offspring from unrelated young[1].

Mistakes in discrimination are most likely for males of internally fertilizing species, especially when the females accept multiple partners. Indeed, in most such species males do not care for young, and it has been suggested that this is because they are uncertain which juveniles are their own. But a new study by Buchan and colleagues[2], described on page 179 of this issue, reveals that when male savannah baboons (*Papio cynocephalus*) intervene in fights between juveniles, they favour offspring over nonkin. This work is important because it reveals that such intervention is a manifestation of nepotism, that paternal care can occur even when females copulate with several different males, and that the kin-recognition mechanisms of a wild primate approach those of humans in precision and sophistication.

In nature, multiple mating is commonplace and widespread, and molecular genetic analyses reveal that it typically results in females bearing the offspring of several males[3,4]. To avoid misdirecting nepotism, males generally rely on indirect cues of their paternity of entire broods[5]. For example, male bluegill sunfish (*Lepomis macrochirus*) are less willing to defend eggs and fry against predators, and more likely to abandon or cannibalize young, if cuckolders had lurked nearby during spawning (a proven threat to paternity) than if they had experienced no cuckolders[6]. However, there has been no evidence that bluegill sunfish, or males in any other wild vertebrate, can distinguish offspring from unrelated juveniles within a given brood[7] — until now.

Buchan and colleagues' study[2] builds upon 30 years of continuous research on the baboons of Kenya's Amboseli Basin, located at the foot of Mount Kilimanjaro. These primates live in multi-male, multi-female troops, in which adult males frequently intervene in fights that break out between juveniles. Such intervention and physical support shields young from injury and stress, and enhances their dominance rank. During 1999–2002, the researchers recorded which youngster was assisted when an adult male baboon intervened in a fight. By analysing DNA from faecal and blood samples the authors established, *post hoc*, whether there was a genetic relationship between each male–juvenile dyad. They report that when males were faced with a choice, they were significantly more likely to support offspring than unrelated juveniles (Fig. 1). Male support of females that are being attacked is a well-known indicator of 'friendship'; it now seems that such behaviour toward youngsters is in fact paternal care.

But how do male baboons avoid misdirecting their nepotism? Two mechanisms are possible. First, males might rely on indirect cues of paternity, as with the male bluegill sunfish that notice cuckolders during spawning. Female baboons are most fertile during the last five days of the follicular phase of their oestrous cycle, which is recognizable by the degree of swelling of their sexual skin. Males might therefore behave according to a simple darwinian algorithm (behavioural rule), such as 'assume that a juvenile is your offspring if you frequently copulated and consorted with (guarded) its mother when her perineum was maximally swollen'. If so, males should distinguish such 'behaviourally predicted' offspring from unrelated juveniles born to females with whom they did not copulate. Moreover, the probability of a male assisting a juvenile should correlate with the proportion of time that the male spent sexually monopolizing its mother during her period of maximum fertility. This is indeed what Buchan *et al.* observed.

A second, complementary recognition mechanism involves a male using direct (phenotypic) cues, such as how a juvenile looks or smells, to assess his likelihood of being its father. This mechanism, known as phenotype matching, is widespread in nature[8], including among primates. In humans, the resemblance of a baby to its mother's husband is a well-known source

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Figure 1 **Paternal love: a male baboon intervenes in a squabble between two juveniles on behalf of his own offspring.**

of interest and familial controversy. But to demonstrate convincingly that males in a given species use self-referential phenotype matching requires researchers to identify the phenotypic cue, alter or obliterate it, and then observe predictable changes in — and even failure of — recognition. Unfortunately, such manipulations are not feasible for wild baboons, and they might also disrupt the 'normal' behaviour of the animals.

Nonetheless, Buchan and colleagues' data indicate that male baboons do use direct as well as indirect cues. As mentioned above, when males intervened in fights between the offspring of females with whom they had and had not consorted, they (the males) consistently favoured the offspring of the former females. In this case, both types of cue — indirect and direct — would be in agreement that one youngster is an offspring and the other is not. But when males intervened in fights between offspring of different consorts, and only one juvenile was actually sired by the male, direct and indirect cues must have been in conflict. Yet, although the males' choices were less decisive, they still favoured true (genetic) offspring over unrelated juveniles. This implies that males do use phenotype matching, and that when direct and indirect cues conflict, the direct cues 'win out'. The authors' previous report[9] that females in this population favour paternal half-sisters over non-kin strengthens the interpretation that phenotypic cues are used to identify kin.

The likelihood of phenotype matching could be explored further by extending Buchan and colleagues' logistic regression approach. The authors partitioned juveniles into three discrete categories — offspring, unrelated but behaviourally predicted offspring, and non-offspring — but probability of paternity is actually a continuous variable. So, one could instead plot the regression between a male's probability of paternity (the proportion of a female's follicular phase that the male monopolized) and the relative frequency of male interventions. If the data points that fell above the regression line — the residuals — represented true (genetic) offspring significantly more often than non-kin, whereas points that fell below the line were the reverse, then this would indicate the occurrence of phenotype matching.

Regardless of the recognition mechanism, it is clear that male Amboseli baboons are fairly certain of their paternity. This casts doubt on the conventional wisdom that female primates copulate with several males to confuse paternity (to reduce infanticide and increase the pool of males that provide care for young). It also raises anew the question of why females typically mate so many times. Perhaps multiple mating enables females to compare males' abilities to stimulate them during sexual encounters[10]. Or it could enhance sperm competition, which would benefit females if more competitive sperm contain 'better' genes, resulting in more vigorous offspring that are more likely to survive and reproduce[11,12]. ■

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Cosmochemistry

Inside the cosmic blender

Alex N. Halliday

The Solar System has a largely uniform isotopic composition but with tantalizing small variations. Geochemists are trying to ascertain the mechanisms and types of stars that produced this state of affairs.

Long before astronomers presented us with spectacular images of the material swirling around other stars, Pierre-Simon Laplace (1749–1827) proposed that the planets of our Solar System formed from a circumstellar disk. The scale and degree of isotopic heterogeneity of the matter in our Solar System provide unique insights into the dynamics associated with the development of these disks, and on page 152 of this issue Becker and Walker[1] highlight some of the problems associated with one class of the isotopes concerned — those of molybdenum.

Modern mass spectrometry techniques had revealed that the isotopic compositions of many of the more refractory elements in meteorites, including a primitive class of meteorite called chondrites, are, within error, identical to those found on Earth itself[2]. It was unclear how the Solar System could have such a uniform composition without some kind of earlier mixing process, because the mechanism that produces these elements creates huge isotopic heterogeneity. The elements heavier than hydrogen and helium ('metals' to astronomers) are manufactured by fusion and irradiation in stars, in a process known as nucleosynthesis. Different kinds of mechanisms produce distinct isotopes, depending on the mass of the star, its stage of development and its metal composition. The most likely way to produce a uniform mix of atoms from the many stars that fed the molecular cloud that eventually formed our Solar System was for the building-blocks of the Earth and planets to have condensed from a hot, well-mixed gas. This idea led to a series of 'hot nebula' models, but various lines of evidence have since shown that such models can only apply to localized portions of the Solar System.

The most important evidence has stemmed from the discovery of presolar grains[3]. A variety of grains condense in stellar envelopes and so record the extreme isotopic composition generated in the star itself. These have been discovered in chondrites — which are now viewed as having formed from relatively cold dust and debris in the circumstellar disk. The development of techniques for measuring the isotopic compositions of these submicrometre specks of stardust has produced data even for trace elements such as molybdenum and zirconium[4]. These remarkable samples of other stars have isotopic compositions that are completely unlike that of our Solar System. But they do match the compositions predicted from theory for various kinds of stars[3,4].

Some types of presolar grain could not have survived the high temperatures and chemistry advocated in the hot nebula model. Therefore, this stardust must have been introduced to a cold disk. There is no obvious mechanism for large-scale mixing in the molecular cloud that preceded disk formation, so such heterogeneity was probably eliminated by mixing in the disk itself, otherwise we could not explain the isotopic uniformity of the Solar System.

Astronomers have found evidence that disks act like swirling conveyor belts, accreting gas and dust onto the central star[5]. Most of the disk consists of hydrogen and helium, and its drag on the dust may result in lateral and radial mixing that eliminates variations[6]. Precise isotopic measurements could potentially allow small variations to be resolved and provide a map of mixing in the