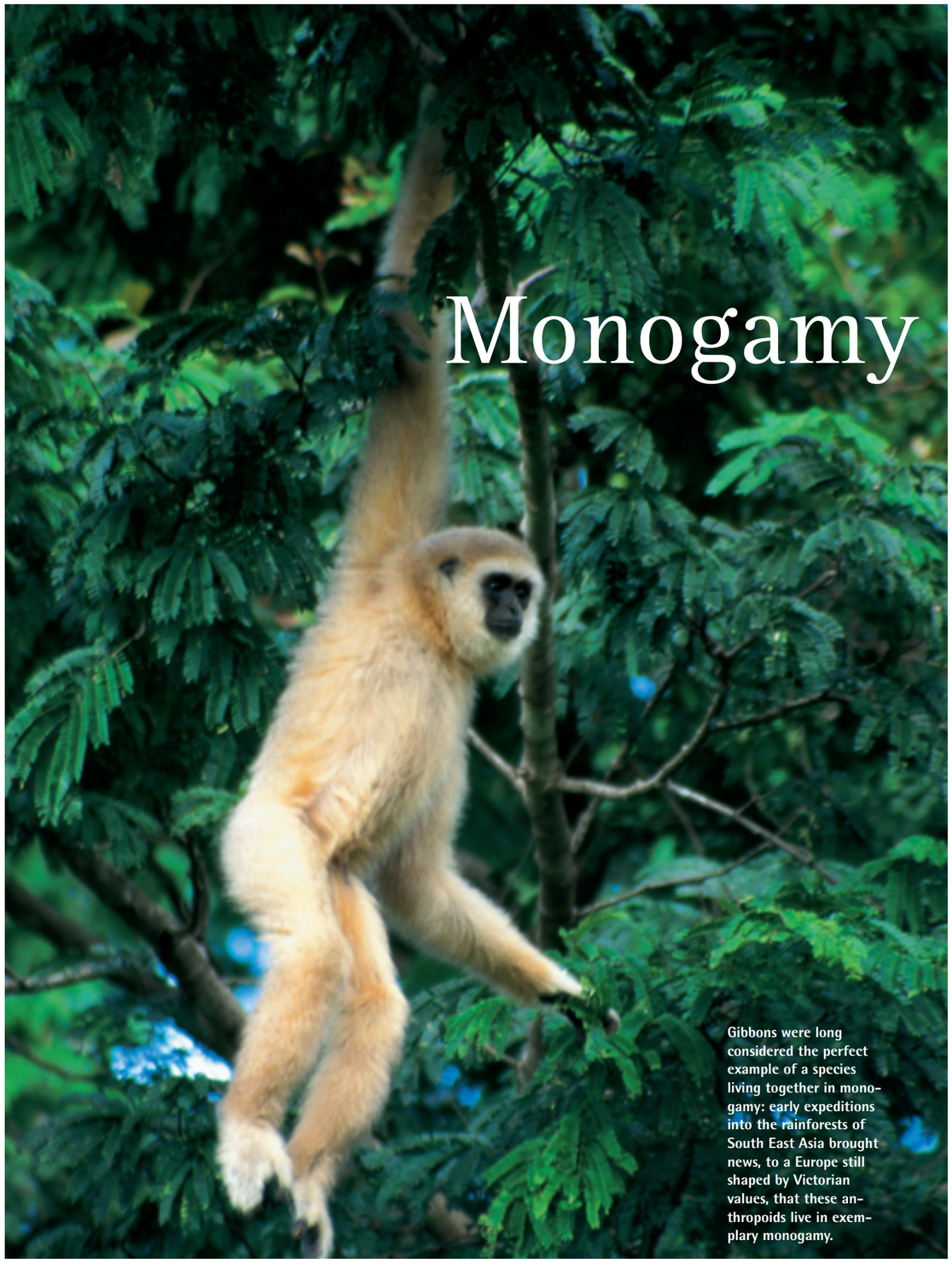

Monogamy – a Variable Relationship

At a workshop entitled "Monogamy: Partnerships in Birds, Humans and other Mammals" held last year in Leipzig, scientists discussed an old topic in the light of new research. **Dr. Ulrich Reichard** *of the* **Max Planck Institute for Evolutionary Anthropology** *has summarised the most important aspects for* MaxPlanckResearch.

Gibbons were long considered the perfect example of a species living together in monogamy: early expeditions into the rainforests of South East Asia brought news, to a Europe still shaped by Victorian values, that these anthropoids live in exemplary monogamy.

Photos: Ulrich Reichard / Corbis

Living together as a monogamous pair, that close social relationship between a male and a female, is relatively rare in mammals, only occurring in around three percent of species. In non-human primates, however, monogamy is clearly more widespread, practised as it is by around 15 percent of species, while, in birds, monogamous pair-relationships are even considered the norm. As for our own species, Murdocks' "Atlas of World Cultures" reveals that some 17 percent of the around 560 societies listed are in some way socially monogamous. Yet the image of the idyllic nuclear family consisting of mother, father and children is deceptive – at least in animal societies: conflicting male and female interests frequently lie hidden beneath the surface of close partnerships and, on closer inspection, the idealised, seemingly harmonious pair-relationship sometimes turns out to be more like a battle of the sexes.

Behavioural observations show that living together in social monogamy does not equate to monogamous mating or reproduction. Thus the females of the Lesser apes, Alpine marmots, fat-tailed dwarf lemurs, aardwolves, common marmosets and small Mongolian gerbils, and many pair-living birds are not too particular about sexual fidelity to their male social partners. Occasional copulation outside the pair-relationship – known as extra-pair copulation (EPC) – has now been fairly well documented in mammals and also a number of bird species. And females from our own species are probably no exception either. Although figures on the incidence of young women from western cultures having socio-sexual relations with more than one male partner at a time vary widely from "occasional" to "more than half" depending on the study, for some women at least, sexual flexibility appears to be quite compatible with stable social partnerships and unburdened by obvious psycho-social difficulties.

The discovery that socially monogamous females actively mate with several males came as a surprise to science. For it was actually assumed that, overall, females reap few reproductive benefits from copulating with several males and none at all if they live in stable pair-relationships. On the contrary: females guilty of sexual infidelity must even expect to be at a disadvantage if their partner sees them. Limited male assistance in rearing offspring may be one result of female sexual flexibility – not to mention parasites or disease which may be caught through the sexual act. John G. Ewen and Doug P. Armstrong (School of Zoology, La Trobe University, Melbourne, Australia, and Institute of Natural Resources, Massey University, Palmerston North, New Zealand) discovered, for example, that stitch-bird males fed their offspring less the more frequently other males tried to copulate with their partners.

Nevertheless evolutionary biologists have got it quite wrong as far

White-handed gibbons in their element: true acrobats, these brachiators swing agilely through the treetops of the primeval forest, up to 50 metres above the ground, searching for fruit, leaves or shoots.

as the monogamous sex life of pair-living females is concerned. This has become clear in recent years through genetic paternity tests which bring to light the consequences of secret sexual activity outside stable partnerships. For a number of years now ornithologists have been checking precisely how many young in the nest of pair-living birds were really fathered by the female's social partner. An astonishing fact emerged as ornithologists Dennis Hasselquist and Paul W. Sherman (Department of Animal Ecology, Lund University, Sweden, and Department of Neurobiology and Behavior, Cornell University, Ithaca, USA) discovered through their comparative analysis of that species-rich group of birds, the sparrows: there is hardly any species of sparrow where the nest does not contain young sired by outside males.

Yet the real surprise was that the proportion of extra-pair young in sparrows living in strict social monogamy was around twice as high as in species where a female can also form a socially polygynous pair, in other words, can live with a male who already has a partner. The ornithologists explain this difference through greater freedom in the choice of partner: where females can choose their social partnerships more freely, those who have opted for a socially monogamous pair-relationship are probably also sexually more monogamous than females of species where social monogamy is the only norm.

What benefits do socially monogamous females gain by reproducing with other males? This is the topic which ornithologist Bart Kempenaers of the Max Planck Research Centre for Ornithology in Seewiesen is currently studying. He makes a distinction between direct, indirect, and social benefits.

Food wins females over

Copulating with several males can be directly beneficial to females if males offer "free gifts" during their advances. These copulation gifts are particularly well-known in insects: thus males of the scorpionfly *Hylobittacus apicalis* give their partners bluebottle titbits at the start of copulation and the longer it takes to consume the fly, the longer copulation continues. Gottfried Hohmann and Barbara Fruth (Max Planck Institute for Evolutionary Anthropology, Leipzig, and Max Planck Institute for Behavioural Physiology, Seewiesen) also noted a connection between gifts of food and mating in bonobos (Great apes). Females presented themselves to males for copulation if the males had a much sought-after fruit.

Another method of obtaining direct material help though copulation was observed by J. David and Sandy H. Ligon (Department of Biology, University of New Mexico, Albuquerque, USA) in the cooperatively breeding green woodhoopoe where, after egg laying, females occasionally copulate with one of the up to four male helpers – evidently to motivate them to collect more food for the female and her young. Yet the clearest indication so far of the material benefits to be gained from copulating outside a stable pair-relationship comes from the red-winged blackbird. Elizabeth M. Gray (Department of Zoology, University of Washington, USA) observed that females who had copulated with neighbouring males were granted access to search for food in the adjoining territory while sexually monogamous females were not afforded this privilege. Moreover, neighbouring males issued more aggressive warnings when predators approached a neighbouring nest if they had copulated with the resident female.

An alternative hypothesis favours indirect genetic benefits from extra-pair copulation. This includes a number of factors connected with the transmission of genetic material. Females profit indirectly from selecting certain copulation partners in that the young fathered by these males will be more able or will, in later life, be more attractive to sexual partners.

A variation of the genetic benefit hypothesis is based on the idea that females copulate with several males to avoid possible infertility on the part of their partner and the associated reproductive loss. Yet, according to Kempenaers, there is some dispute about this "fertilisation insurance hypothesis" as an explanation for promiscuous behaviour. The researcher worked with blue tits some years ago and discovered a different reason for promiscuous behaviour: if males differ in their genetic make-up, then it should be beneficial for a female paired with a male of relatively poor genetic quality to increase her offspring's chances of survival and reproduction through extra-pair copulation with a male of higher genetic value. This supposition has become established in the scientific literature as the "good genes hypothesis", although individual genes cannot be selected in the genetic process. Rather what is meant is a number, a combination of characteristics which promises the individual greater success in the competition for reproduction. In the past, though, it proved difficult, particularly with birds, to confirm this seemingly plausible hypothesis.

Photos: Ulrich Reichard / Corbis

However, Kempenaers and his colleagues succeeded in obtaining evidence in blue tits. The scientists took the frequency with which females visited a male's territory as an indicator of that particular male's attractiveness. The more frequently a male received females in his territory, the more attractive he was classed. It emerged that females paired socially with attractive males did not leave their partner's territory during their fertile period, while females paired with a male classed as unattractive frequently visited neighbouring territories during their fertile period. And this observation was also reflected in the genetic analysis.

One question remains unanswered, however. How do females identify the genetic qualities of males when only external phenotypical characteristics such as appearance or behaviour are available to them? In a study of the great reed warbler, Dennis Hasselquist, Staffan Bensch and Torbjörn von Schantz (Department of Animal Ecology, Lund University, Sweden) found that females preferred neighbouring males with a particularly extensive repertoire of songs for copulation outside the pair-relationship. It also emerged that more juveniles fathered by males with larger repertoires survived to adulthood than offspring of fathers with a more limited repertoire of songs. The researchers concluded from this that female great reed warblers can reliably deduce from a male's song the chances of survival of the young he fathers.

Alongside the "fertilisation insurance" and "good genes hypothesis", other explanations for extra-pair copulation are discussed. Thus genetic compatibility of sexual partners or production of genetically different offspring could also play a part. All in all, it appears unlikely that the complex reproductive behaviour of pair-living females can be explained by one single answer. The differences in function of sexual behaviour in different species appear too large. Moreover, the hypotheses are not entirely mutually exclusive and probably only explain the observations when in combination.

Partner testing before the next breeding season

According to Richard W. Wagner (Konrad Lorenz Institute for Comparative Ethology, Vienna, Austria), the fact that opinion is not yet clear on the possible genetic benefits of extra-pair copulation for pair-living females could also indicate that sexually promiscuous behaviour on the part of pair-living females should not be considered solely in connection with reproduction. This conclusion is suggested by his studies of the small razorbill. He observed extra-pair copulation during two phases in the female reproductive cycle both outside the females' fertile period: females either copulated with outside males directly after egg laying and/or at the end of the mating season. Wagner interprets this non-reproductive sexual behaviour in the long-lived razorbill female who is extremely loyal to her nest site as a form of partner test for the coming breeding season.

The risk of infanticide – the murder of an infant – is also under discussion as a reason for sexual contact between pair-living females and outside males. Infanticide can be a successful male reproductive strategy if three conditions are met simultaneously: there should be no, or virtually no, chance that the "child-murdering" male fathered the young; in addition, the mother of the dead offspring should be ready to conceive again sooner, and finally, the male should have an increased chance of fathering the female's next offspring.

According to the hypothesis, pair-living females possibly copulate with several males simply to conceal the paternity of their young. If the paternity of the young is uncertain, if therefore a male runs the risk of killing his own offspring, the risk of infanticide is virtually reduced to zero. This hypothesis has so far only been indirectly proven in socially monogamous mammals and is unlikely as an explanation for promis-

Dikdiks practise social monogamy as an extreme form of mate guarding.

cuous behaviour in pair-living birds, not least because infanticide is rare in birds, while extra-pair copulation in socially monogamous females is common.

Monogamy researchers are looking into how pair-living evolved in the first place. Carel P. van Schaik and Peter Kappeler (Department of Biological Anthropology and Anatomy, Duke University, Durham, USA, and Department of Behavioural Research/Ecology, German Primate Centre, Göttingen) are convinced that pair-living was derived from living alone and that there was subsequently a transition from flexible to stable pairs. Pair-living must be the preferred strategy for both partners here: either because both partners prefer it or because one partner prefers it and the other is unable to alter the system in their favour. It is assumed in the case of the second alternative that, over the course of time, the reproductive biology of the partner, who would in principle have preferred a different form of partnership, evolves so that they adapt, increasing their fitness as a result of stable pair-living. In the end living in stable pairs is beneficial to both partners.

These evolutive changes in behaviour or reproductive biology may, for their part, bring new selective benefits. Van Schaik and Kappeler see the most likely benefit in the evolution to stable pairs as the development of direct male assistance in rearing young: they advocate the theory that the crucial contribution made by pair-living male primates lies in guarding against infanticide. They reach the conclusion that, in the past, the only plausible pacemakers for the evolutive leap from flexible to stable pairs were reducing the risk of infanticide in the case of primate females living gregariously and reducing the risk of predators by nest guarding in the case of solitary living females, and that both aspects are also crucial for maintaining pair-living.

Peter N. M. Brotherton and Petr E. Komers (Department of Zoology, Cambridge University) deny, however, that the development of pair-living is necessarily linked to mutual concern for offspring. They studied the dikdik, a small species of antelope which lives in socio-genetically monogamous pairs. Single young are born and hide in low bushes until they can follow their mothers. Males do not help directly in rearing the young. According to Brotherton, only one of the hypotheses on the evolution of social monogamy applies to the dikdik: social monogamy evolved as an extreme form of mate guarding.

Examples from the animal world clearly show that social, sexual, and reproductive relationships are complex and varied, even in socially monogamous species where hitherto "monogamous" appeared the only term necessary to describe structures resembling the nuclear family. The workshop revealed that an explanation for sexual flexibility cannot always be found. And one question will continue to preoccupy us humans: what about socio-sexual monogamy in homo sapiens? Data on biological aspects of human reproduction are difficult to obtain. Humans are harder to observe than animals which is why structures of sexual relations are best accessed indirectly by asking questions. As a result, "hard" data are susceptible to error. Experiments are only feasible to a limited degree and large-scale representative genetic studies of paternity are so far virtually non-existent. It appears debatable whether empirically reliable findings, similar to the results for birds and other mammals, can ever be collected on human reproductive behaviour.

Man caught between nature and culture

Intercultural comparison, however, offers one way of tracing the phenomenon of monogamy in human societies, where a fundamental difference between studies on animals and humans can be observed, as Bobbi S. Low (School of Natural Resources and Environment, Michigan University, Ann Arbor, USA) remarked. For while reproductive strategies and the mating system can be studied directly in animals, in human societies researchers must often be content with studying marriage systems. These levels of analysis are unequal since marriage systems represent cultural developments. Marriage rules generally determine how many partners can be taken at one time and when, for example, marriageable age is reached. The interests of third parties possibly play a decisive role here; as well as the couple themselves, parents and relatives often pursue their own interests and directly influence the socio-reproductive behaviour of couples.

Photos: Okapia, Munich

Although, in many animals, social monogamy appears closely linked to ecological conditions, where it is more worthwhile for males to concern themselves with providing for offspring than to go looking for a mate, Low found no such connection in human cultures. She also observes that societies in which men signal their married status and thereby their unavailability frequently practise social monogamy. These societies are predominantly characterised by strong ecological constraints which would not allow men to live in social polygyny anyway.

Social monogamy became increasingly more widespread in western cultures during industrialisation as it became harder to feed the family, and social polygyny became less and less beneficial to men. Monogamy probably follows the same rules in man as in animals, Low concluded – it is perhaps just a bit more complicated. Whether this summing up also included promiscuous sexual behaviour in the females of many pair-living animal species was uncertain.

So far we can only speculate whether women in societies geared strictly to living together in monogamy make more frequent use of their secondary partner choice potential and have children with men other than their social partner more frequently than in societies where free partner choice is the norm. It is a subject which novels, films, and the tabloid press love to tackle. And what is more, if we take what we read in the gossip columns of the glossy magazines with a pinch of salt: that feeling of jealousy perfectly (or should that be: uneasily) familiar to most people is perhaps the surest sign that one can never be completely certain about one's partner, despite marriage certificates and contracts.

The term monogamy was not redefined at the workshop, but it was refined: however, there remains a large area of which only a small part is clearly defined. What did become clear, however, was the variety and flexibility within that group of animals usually collectively referred to as "monogamous" due to their pair-living. The important result which emerged from the conference was actually recognition that monogamous life forms are immensely varied.

A number of studies of birds show that living together in monogamy is not the same as reproducing in pairs. The small number of pair-living mammals whose genetics have been studied so far reveal a surprising continuity between social and genetic systems. Only occasionally were extra-pair young found in socially monogamous mammals. The reason for this difference remains uncertain: it may reflect the underlying difference in the proportion of monogamous systems in birds and mammals. Birds live predominantly in social pairs, yet only a small proportion of mammals are socially monogamous. It is conceivable that pair-living only developed in mammals where male and female reproductive interests are very similar. The difference may also lie in the conditions for social monogamy.

Monogamy beneficial "in the long term"?

While male birds often perform the same tasks as females in providing for the young by incubating the eggs and feeding the offspring, male mammals are largely relieved of the task of providing directly for their offspring by lactating females. It is possible that this impedes the development of a socially monogamous system in mammals, thereby making it easier for males to assert their basic socio-sexual polygynous tendency over females. Moreover, female birds can store sperm and obviously use it at just the right time to fertilise an egg. This female option of manipulating biological paternity is not open to female mammals or, if so, only in certain cases – a fact which could make genetic partner selection following social partner selection more difficult and thus might bind social and genetic monogamy together.

In tree sparrows, relationships frequently last only one breeding season; they pair afresh each spring.

Perhaps there is also a link between reproductive monogamy and the longevity of many mammals compared with birds. Genetic monogamy also appears more widespread in birds where partners stay together for many years. This distinguishes the majority of pair-living mammals from many sparrows, where pairs frequently only live together for one breeding season and pair afresh each spring. The situation is quite different in mammals and particularly in primates whose social relations are designed to last long periods of time. Here, social partners know each other well and repeatedly interact with one another. It is possible that this creates conditions which also made genetic monogamy beneficial where social monogamy developed. This could ultimately mean that longevity and enduring social pair-relationships perhaps offer good pre-conditions for socio-genetic monogamy.

Ulrich Reichard