who's your Daddy?

MATING STRATEGIES IN BIRDS

‘I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection’

CHARLES DARWIN, 1859

The basic tenet of Darwin's Theory of Natural Selection is that only the fittest individuals will survive. A necessary corollary of this is that these are the individuals that will leave the greatest legacy in terms of the number of progeny they produce. However, a number of factors are likely to influence the strategy or strategies an individual will employ to try to maximise its lifetime reproductive output and hence its genetic footprint on subsequent generations.

In this article, **PHIL HOCKEY** examines some of these strategies, which range from the normal to those unlikely to be sanctioned by many churches.

ALBERT FRONEMAN

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IN THE PERFECT FEMALE WORLD, the perfect female strategy would be to mate with as many males as possible and then to leave the temporary lovers to incubate the eggs and raise the young. In the perfect male world, however, the optimal solution is exactly the opposite, with the result that the two 'ideals' are in direct conflict with one another and cannot co-exist within a single species. The ultimate compromise, of course, is monogamy, whereby a single male and a single female remain together for at least one breeding season and in some way share the burden of rearing their young: both the male and the female have lost the same proportion of their respective, strategic Shangri-Las.

Previous spread *The African Jacana has a very rare breeding strategy, termed polyandry, in which a single female lays clutches for several males and then leaves all incubation and chick-rearing duties to her mates.*

MONOGAMY

Social monogamy (that is, the appearance of being paired and 'living together') is practised by the majority of the world's birds, perhaps as many as 80 per cent of species. But, even within a monogamous relationship, there is much variation in the ways in which the workload of breeding is (or, in some cases, is not) shared between the sexes. Some species are monogamous because the female would be unable to incubate and rear young without male assistance. Large albatrosses, for example, breed on remote oceanic islands that are often far from food sources. As a result, foraging trips are long, often lasting a week or more, and during this time, the partner must remain at the nest.

Monogamous Black Sparrowhawks *Accipiter melanoleucus* share the workload in a different way. The female does all the incubation, during which time the male defends the territory and brings food to the female on the nest. Once the chicks have hatched, and even beyond fledging, the male continues to act as provisioner and the female as guardian.

Among territorial species, quality of the area is also thought to promote monogamy. If territories vary greatly in terms of the quantity and quality of their resources, males defending the top-quality properties may be able to attract more than one female. But if all patches contain roughly equal resources, then monogamy is likely to be (and indeed is) the norm.

But defence of a territory is not necessary for monogamy to occur. Many male ducks, including the alien Mallard *Anas platyrhynchos*, are much more concerned about defending a mate than protecting a territory. The reason for this is that they have largely excused themselves from breeding duties, neither incubating eggs nor caring for the brood. These activities are the lot of the female and, not surprisingly, females have a higher mortality rate than males as a result. This in turn leads to a skewed sex ratio, with males outnumbering females. The consequence of this is not difficult to imagine, with surplus males constantly on the lookout for mating opportunities, while paired males have to spend most of their time guarding their mates to make sure this doesn't happen.

ABANDONMENT & ADULTERY

But nature is fickle. No sooner does an apparently successful strategy evolve, than someone's out there trying to cheat the system. Some of the best-known examples of this relate to mimicry, whereby a sneaky mimic evolves to look like another (model) species that is either distasteful or dangerous. The catch with such a strategy, of course, is that the mimic is destined to be rarer than the model, because otherwise predators would realise that they are being conned and the arms-race pendulum would start to swing in the opposite direction.

Deception is alive and well in the mating game. The aim of the deception is to pass on the maximum amount of genetic material with the minimum amount of effort. In this respect, females are worse off than males, because eggs are energetically expensive to produce relative to sperm. If a female can produce only a finite number of eggs in a breeding season, then her best option is to parasitise someone else's parental care. The best way of achieving this is to sneak an egg into someone else's nest and to leave the host with the energetic cost of incubation and chick-rearing. This behaviour is quite widespread among birds that are not traditionally considered brood parasites, such as Common Starling *Sturnus vulgaris* and Common Moorhen *Gallinula chloropus*. In an analysis of 89 non-parasitic species, 21 per cent were found to practise egg-dumping, at least occasionally: typically, these were species capable of laying large numbers of eggs. The logical end-point of this female deception is obligate brood parasitism, as practised by most cuckoos, and by all honeyguides and indigobirds.

Males are not constrained by the energetic costs of egg production, and it is to their advantage to mate with as many females as possible (even though they are in an apparently monogamous relationship). Assuming fertilisation is successful, at least some of the cuckold's genetic material will be carried to the next generation without any further effort on his part. Studies of Zebra Finches *Taeniopygia guttata* in Australia suggest that the male that copulates last with the female will fertilise about 80 per cent of the eggs.

Prior to the advent of modern 'forensic' genetics, the full extent of male cuckoldry was not appreciated. Although about 80 per cent of species are socially monogamous, only about 25 per cent of these are strictly sexually monogamous. Extra-pair copulation (a fancy scientific term for adultery) occurs so frequently, even in socially monogamous species that, on average, 11 per cent of offspring are sired by someone other than the resident male. To date, the record-holder for infidelity and promiscuity among socially monogamous species is the northern European Reed Bunting *Emberiza schoeniclus*: in one study, 86 per cent of broods contained at least one chick fathered by an 'outsider', and 55 per cent of all chicks were fathered by outsiders.

However, while the promiscuous male is out and about dispensing his sexual favours to the mates of others, he runs the real risk that another male is around and about doing exactly the same to his mate. This is where some level of autoregulation enters the system. There are really only two options for a male to avoid being cuckolded: either he must spend most of his time guarding his mate (which reduces the time available for extra-curricular activities) or he must copulate with his own mate so frequently that the probability of his sperm fertilising her eggs is very high. The latter strategy is adopted by the Northern Goshawk *Accipiter gentilis*. For each clutch laid, the resident male copulates between 500 and 600 times with his mate (which probably doesn't leave him a whole load of energy to cuckold anyone else).

WARWICK TARBOTON (2)

It's amazing what some hosts will accept, such as these single Red-chested Cuckoo Cuculus solitarius *eggs in the nests of White-browed Scrub-Robin* Cercotrichas leucophrys *(***above***) and Kurrichane Thrush* Turdus libonyanus *(***top***).*

Opposite *The need to both guard and feed their chick has forced large albatrosses, such as the Wandering Albatross* Diomedea exulans*, to be monogamous.*

CHRIS VAN ROOYEN

HEDGING YOUR BETS...

Even the apparently honest male mating strategy involving a good territory and lots of mates is open to abuse. The **European Pied Flycatcher** *Ficedula hypoleuca* is a case in point. At the start of the breeding season, once the seemingly monogamously mated female has started laying her clutch, the male moves off elsewhere and starts advertising for a second female. If he finds one, he waits until she too has started to lay, at which point he returns to the original female and helps her raise the brood, abandoning the bigamous partner. Needless to say, the success of the second female is much lower than that of the original. The Pied Flycatcher is a migratory species, and it appears that most of the 'second females' are birds that have returned late from migration and are not too fussy about the quality of the male with which they choose to mate.

RAY TIPPER

MALES WITH MULTIPLE MATES – HONESTY & DECEPTION

If a male or a female can acquire multiple mates, this is termed polygamy, and it is one step closer to the 'perfect world' than is monogamy. A male with several mates is described as polygynous.

The most common form of polygyny involves a male defending a resource-rich territory to which he is able to attract several females. In polygynous mating systems, it is not unusual for some males to succeed in attracting several mates while others attract none. At face value, this presents a conundrum: why should a female settle in a territory where there are already several other females (which are potential competitors) rather than choose an as-yet unmated male? The latter option would apparently give her greater access to male assistance while breeding. The answer lies in the quality of the territory: in really good territories, females are better off sharing with other females than they would be settling on a poorer territory and having to share its resources only with her mate. Among southern African birds, polygyny is not a common strategy, being followed by only 32 species; of these, 20 are euplectids (weavers, queleas, bishops and widowbirds) and seven are bustards or korhaans. The remainder are a taxonomic mishmash, including Common Ostrich *Struthio camelus*, the buttonquails and Pennant-winged Nightjar *Macrodipteryx vexillarius*.

If the 'good territory' strategy for achieving polygyny could be equated to owning a baronial mansion, the alternative is more analogous to a pick-up joint. This alternative is a form of wild, sexual advertising, called lekking (derived from the Swedish word *leka*, meaning to play). Leks are areas where males gather and display together, each on a small territory (usually close together, but sometimes a hundred metres or more apart) containing no resources. Females visit these leks to select a mate, but a very small proportion of all males present often gain the majority of the matings; in a study of 14 colour-ringed Village Indigobirds *Vidua chalybeata* in one dispersed lek, one male obtained more than half of all matings.

One feature that characterises lekking species is that the females must be able to incubate the clutch and rear the chicks without any assistance from the male.

JARI PELTOMÄKI/NHPA/PHOTOSHOT

This is possible if the species is precocial, with self-feeding chicks (for example, Ruff *Philomachus pugnax* and Great Snipe *Gallinago media*). It is also possible if the brood is very small and/or food is very abundant and, of course, if the species is a brood parasite (such as Village Indigobird).

For a male to compete successfully at a lek, he must demonstrate, usually through elaborate display, that he is a better male than his neighbours. In the case of Great Snipes, females respond to the amount of white in the tail, whereas in the case of Long-tailed Widows *Euplectes progne*, they respond to length of the male's tail. The latter has been demonstrated experimentally, where males with artificially lengthened tails improved their mating success, while those with artificially shortened tails had reduced mating success.

But if females select only the best males and it is these genes that are passed on, why aren't all the males perfect? This has long puzzled scientists, to the point where it has even been given its own name – the 'lek paradox'. The issue is still not fully resolved. It is true that the combinations of genes controlling exaggerated sexual traits are complex, and it has been hypothesised that variability among males is maintained by genetic mutations. However, a series of experiments with a lekking butterfly has raised another possibility. If mate choice by females involves a cost to the female, they themselves may vary in their ability to meet this cost, resulting in some females making less-than-perfect mate choices, giving less-than-perfect males a chance to pass on their genes.

TURNING THE TABLES – FEMALE EMANCIPATION

When a female mates with several males, it is termed polyandry. This is the rarest form of mating system and differs from all others in that females compete for access to males, and mate with multiple males, rather than vice versa. As a corollary, several polyandrous species exhibit reversed sexual dimorphism, with females being larger and/or more brightly coloured than males, as seen in the Greater Painted-snipe *Rostratula benghalensis*, African Jacana *Actophilornis africanus* and Black Coucal *Centropus grillii*. The evolutionary origins of polyandry probably lie in double-clutching by monogamous birds, whereby the female lays two clutches, the first of which is tended by the male, the second by the female: this is practised by Temminck's Stints *Calidris temminckii*. ▷

Above *At the start of the breeding season, male Ruffs develop unique and elaborate head and neck feathering. This is the advertising equipment that they take to leks, where they display in an attempt to attract as many females as possible.*

Opposite *Like many ploceids, male Southern Masked-Weavers* Ploceus velatus *display below their nests in an attempt to attract multiple females.*

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Above *Size is everything! In the case of the male Long-tailed Widow, the number of mates he can attract will depend on the length of his tail.*

Opposite, top *In polyandrous species, the female typically is larger and/or more brightly coloured than the male. This size dimorphism is illustrated here by Black Coucals.*

Opposite, bottom *Australian White-winged Choughs are very unusual in that they appear to cooperate in groups to enable one pair within the group to breed successfully.*

Laying clutches for multiple males is a step not too far removed.

Despite being a rare mating system (probably less than 50 species worldwide), polyandry occurs in four distinct forms. Probably the most common, and practiced locally by Greater Painted-snipe, African Jacana and Striped Crake *Aenigmatolimnas marginalis*, is sequential (or serial) polyandry, in which a female lays eggs for one male, then courts another. In years of good flooding, when clutch survival is high, one female African Jacana may lay eggs for up to seven different males. In dry years, when water levels are low and predation rates high because nests are readily accessible, the dominant male may lose clutches so fast that he ends up receiving all the clutches laid during the season, and the mating system thus becomes monogamous.

American Jacanas *Jacana spinosa* have a rather different strategy, termed simultaneous polyandry. The female defends a territory, within which several males hold smaller territories. The female rapidly mates with all the males and lays eggs in each of their nests (bad news for the males, who cannot guarantee fatherhood of their clutch). In order to ensure that she has plenty of males available in her territory, the female even helps her males defend their territories against one another. Interestingly, the Lesser Jacana *Microparra capensis* is monogamous.

A third form of polyandry, called co-operative polyandry, occurs when a female mates with more than one male and all partners assist in raising a single brood. This behaviour is probably best known in Galapagos Hawks *Buteo galapagoensis*, but has been recorded for other species, including Common Tern *Sterna hirundo*. Locally, in the 1990s, it was discovered that Southern Pale Chanting Goshawks *Melierax canorus* also form polyandrous trios on high-quality territories in South Africa's Little Karoo. Because of the additional help available at the nest, polyandrous trios are more likely to lay a second clutch after successfully rearing a first than are monogamous pairs.

One of the most complex twists to the polyandry story is when females in a population are polyandrous and males in the same population are polygynous. Females only have one active nest at a time, but this may contain young fathered by more than one male, and males may provision at more than one nest. This also goes by the most complex name: polygynandry. There are not many demonstrations of this, but it has been shown for Smith's Longspurs *Calcarius pictus* in Canada, Alpine Accentors *Prunella collaris* in Poland and Dunnocks *P. modularis* in Britain.

BUT WHAT IF I'M GETTING NO SEX AT ALL?

The most evolved primates on the planet have solved this dilemma in a number of ingenious ways, but these are not options available to animals living under the cloud of natural selection.

Deferred breeding is not unusual in birds – some frigatebirds may not breed until they are more than 10 years old – but the usual reason for this is that they have not developed the skills that would provide them with the surplus energy needed for breeding (for example, they would be unable to provision both themselves and their offspring).

One group of birds that has been the focus of massive debate over the past 30 years is what is loosely termed co-operative breeders. These are species that live in groups, usually comprising a single, dominant breeding pair, with other group members being offspring from previous broods (and sometimes unrelated birds). The hangers-on, or helpers, assist in raising the brood of the dominant pair even though they themselves may be physiologically capable of breeding. This type of social system – and it is an ancient one – is confined to altricial species (those that remain in the nest as chicks), and its evolution must have been preceded by the development of intense parental care (which itself was almost certainly a prerequisite for the evolution of altriciality).

A handful of species, including White-winged Chough *Corcorax melanorhamphos* in Australia and Yellow-billed Shrike *Corvinella corvina* in central and West Africa, appear to be obligate co-operative breeders, meaning that the breeding pair cannot raise their young without helpers. Most co-operative breeders, however, are facultative, in that, given good conditions, the dominant pair can raise their young alone. Many hypotheses have been tested about why sexually mature birds should remain in a group where the only chance they have of breeding is if the same-sex adult of the dominant pair dies (and even then they have to wait their turn within a dominance hierarchy). Some do disperse and take their chances at playing the waiting game in a smaller group with a shorter queue. Others stay at home – perhaps because the risks of dispersing alone are very high or because a shortage of nest sites forces group living.

Whatever the ultimate driving factors – and they are likely to differ between species – one Darwinian truth remains. If environmental or social factors prevent a sexually mature bird from breeding, the next best option (in terms of leaving a genetic legacy) is to help individuals who carry some of the same genes as you do (that is, your parents and siblings). It may be no substitute for sex, but it is a vicarious means of helping to pass on at least some of your genetic material to future generations. □

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