COLOUR CODING

Plumage variation within species

Understanding why a small proportion of the world's birds occur in more than one colour form has fascinated ornithologists for decades. In this article **PHIL HOCKEY** and **ARJUN AMAR** of the Percy FitzPatrick Institute explore just how far scientists have come in the search for a unifying theory to explain the phenomenon.

Many bird species show variation in plumage, reflecting differences in age, sex or season. Large gulls, for example, take three or four years to acquire full adult plumage. There are various possible explanations for this, including the signalling of status. It may be in your best interest, if you are not sexually mature, to indicate that you are not a threat to those individuals that are mature. You are then less likely to end up in a fight that you are all but guaranteed to lose.

A number of species also exhibit plumage differences between the sexes – termed sexual dichromatism ('two-coloured'). In instances where this occurs, it is usually the male that is more brightly coloured, as this is interpreted as a trait necessary for attracting the opposite sex. These bright, conspicuous colours and, in some species, elaborate plumes (which reduce manoeuvrability) can result in males being more at risk of predation than females are. Evidence in support of this is the speed with which many brightly coloured males (especially among passerines) lose their coats of many colours as soon as the key business of mating is completed. In many species, males moult from gaudy to well camouflaged, becoming all but indistinguishable from their drabber mates. Although females may also compete for mates, they are more likely to be constrained in the development of elaborate plumage by the need for concealment during incubation. ▷

ALBERT FRONEMAN (2)

Birds of prey, such as these Wahlberg's Eagles, are well represented among the world's polymorphic birds.

ALBERT FRONEMAN (2)

GOOD GENES, BAD GENES
and Darwin's precept

Within sexually mature birds, some species use variation in plumage qualities to signal information to others about an individual's quality; such characteristics may only evolve slowly over time. For example, the bibs of male House Sparrows and the breast bands of male Bar-throated Apalises vary in size between individuals. These ornaments signal social status, with older or more dominant birds sporting larger bibs. Males with large ornaments are favoured by females and, as a result, these males typically enjoy higher-than-average reproductive success. Individuals can also vary in the intensity of their coloration. Male Blue Tits with the brightest blue heads, which shine as beacons to their potential mates (they can see in the ultra-violet spectrum), are more successful than less 'reflective' males.

However, there is another form of plumage variation whose cause or function is more difficult to explain. In some species, birds of the same age or sex can vary dramatically in plumage from one another – this is termed polymorphism ('many-coloured'). Breeding male Ruffs, for example, exhibit extraordinary variation in the colour of the elaborate head and neck plumes that they display to females at communal leks. Surely this flies in the face of Darwinian theory that natural selection should force convergence towards the best-adapted form for the prevailing conditions? The reason could be that the combinations of genes that control these plumage traits are complex: small changes in gene structure may continuously throw up substandard males. More recent research, however, suggests that the problem of poor males may lie at the doorstep of less-than-discerning females. If females incur costs while choosing males (for example, through competition with other, more dominant females), this increases the likelihood of their making less-than-perfect choices and passing less-than-perfect males' genes through to the next generation.

On average, the genes of less gaudy males are more likely to be diluted or weeded out of the population than those of the more spectacularly adorned. In the case of Ruffs, male plumages are so variable that the phenomenon can be termed 'continuous polymorphism'. This is equivalent to a bird that could be dark red, pale yellow or any shade in between. If, by contrast, there was a bird that was dark red or orange or pale yellow but no shades in between, this would be termed 'discrete polymorphism'. Examples of discrete polymorphism among African birds include the dark- and pale-breasted morphs of Jacobin Cuckoo, Gabar Goshawk and Ovambo Sparrowhawk. In a very few Crimson-breasted Shrikes and Black-collared Barbets, the red colour is replaced by yellow. This is not polymorphism in the strict sense; rather it is a genetic accident resulting in a pigment deficiency and is known as 'schizochroism'.

Overall, polymorphism in birds is fairly rare, occurring in fewer than three per cent of Africa's species (see page 41), which is similar to the proportion globally. Taxonomically, it is also far from random: it is found mainly in predatory birds, with seabirds, raptors, owls and bush-shrikes being disproportionately well represented. The fact that polymorphism is present in both modern and ancient families of birds (and is also absent in some ancient and modern families) indicates that it has evolved independently on several occasions and is not simply 'evolutionary baggage' that some species have retained and others lost.

Top *The black breast band of the male Bar-throated Apalis signals both age and territory quality. Males with the largest breast bands defend the smallest territories, but these territories are very rich in food resources.*

Above and right *The two colour forms of the Crimson-breasted Shrike do not represent true polymorphism, but rather a pigment deficiency in the yellow-breasted form (a condition called schizochroism).*

GRANT REED

PETER STACEY

The offspring resulting from the mating of these Gabar Goshawks will be either grey or black, but nothing in between.

Among the species with discrete polymorphism, several (such as the Southern Giant-Petrel) possess one morph that is very much rarer than the other. This is indicative of the rare morph being a recessive condition. In the simplest genetic terms this means that the species carries a dominant (A) and a recessive (a) gene. In the case of the giant-petrel, A = black and a = white. If a youngster inherits one gene from each parent, it could have any one of four combinations: AA, Aa, aA, or aa. The first three will produce a black plumage colour because the dominant gene (A) overrides the recessive gene. The fourth (the double recessive, aa) will produce a white colour because there is no dominant gene to override it. But not every black parent will carry the recessive gene, because it confers a potential disadvantage to that bird's offspring. Even if both parents are black but carry the recessive gene (that is, Aa), their offspring have only a one-in-four chance of being 'aa' (that is, white). And if a double recessive mates with a double dominant (AA), all the offspring will be black. The rarer the recessive gene becomes in the population, the smaller the chance there is of any offspring being the rare morph. This same set of simple mathematics explains why white tigers and white lions are so rare in the wild, but why mating white with white in captivity will produce white offspring. ▷

BARRIE ROSE

HUNTERS AND *the hunted*

Above and above, right *Most Southern Giant-Petrels are dark. The rare white morph is not an albino, but represents a rare double-recessive condition.*

In South Africa and Spain, about 80 per cent of breeding Booted Eagles are pale morphs, suggesting that this colour has a selective advantage over the brown morph in these areas. By the same token, however, being the brown morph is not such a disadvantage that the brown gene has been completely weeded out of the population (and it is even possible that there is no disadvantage in being brown, but more about that later). In Ovambo Sparrowhawks, by contrast, only one to two per cent of birds are black.

In several species, morph ratios vary across the geographical range. Among Gabar Goshawks, for example, black morphs constitute between seven per cent (in the Kruger National Park) and 26 per cent (in south-eastern Swaziland) of the population. Some multi-species studies have shown that where such gradients exist in morph ratios, the darker morphs become progressively more prevalent in increasingly cloudy habitats at high latitudes and altitudes. It is interesting to observe, however, that polymorphism in Parasitic Jaegers and Southern Giant-Petrels follows the reverse trend.

Continuous polymorphism seems to be very much the domain of the hunters – raptors and owls – and especially those that hunt in low light or at night (see page 41). Most of these are coloured in the brown-black-grey-white spectrum. Scops-owls, for instance, fall along this continuum and are intricately patterned: these differences may have arisen to allow them to explore a diverse suite of sites for roosting during the day, when they themselves are potentially at risk from other predators. A grey bird is perhaps more likely to roost in a grey-barked tree than is a brown bird (and vice versa). Another somewhat surprising possibility, given that scops-owls hunt at night, relates to improved hunting success that different morphs may enjoy when targeting different prey species, as has been shown to be the case for Barn Owls in Europe.

But what about the diurnal and crepuscular hunters? Take the Bat Hawk for example, a super-specialised hunter with a very narrow prey spectrum (bats) and a very short window of time in which to hunt (the gathering darkness). Surely that combination of ecological constraints should lead to only one blueprint for success? Yet, no – some Bat Hawks are largely pale underneath, while others are wholly black. Is this

PER HOLMEN

because they wait until it is so dark before they hunt that their less-than-hawk-eyed prey cannot detect one morph any more successfully than another? Or do the different morphs have different hunting success at different stages of the short African twilight – do pale-bellied birds hunt that little bit earlier? Probably not, because even pale-bellied birds have dark underwings and it is unlikely that any of their prey could discern more than a silhouette. Similarly, in a study of Parasitic Jaegers stealing food from Common Guillemots, whether the jaeger was dark- or pale-bellied did not influence its success rate.

The polymorphism in Black Sparrowhawks is similar to that of Bat Hawks. The sparrowhawks display extreme size dimorphism, with females being much larger than males, but both sexes show the same diversity in coloration: some birds have wholly black underparts whereas others are mostly pale below. Especially when breeding, these birds hunt in the murky, pre-dawn light; maybe darker birds have an advantage at this time, whereas paler birds are more successful after the sun has risen and their whiter underparts provide more camouflage against the pale sky. Or perhaps one morph has better hunting success in more wooded habitat and the other in more open terrain?

Another intriguing suggestion for the persistence of polymorphism is that it pays to be the rare morph because this provides an added element of surprise. This suggestion was thought to be particularly relevant for diurnal, carnivorous species that prey on moderately intelligent creatures with good predator-detection skills. If prey animals develop a search image for a particular colour of predator, then a predator may gain an element of surprise if it is coloured differently to the average as the prey may take slightly longer to recognise the threat. And when it comes to surviving or succumbing to a predator attack, milliseconds can make all the difference.

The concept of 'standing out from the crowd' is not a new one. Back in the 1960s, the advantage conferred on 'oddities' was termed 'apostatic selection' (from Greek, meaning 'a deserter'). The logical end point of such selection is that every individual looks different. Apostatic selection did enjoy a period in the scientific limelight, but perhaps it was doomed as a concept when Mediterranean sand mussels, almost all of which are patterned differently, were used as an example. In this instance, birds that preyed on the mussels were believed to be the agents of selection. The fundamental flaw in this argument, of course, is that sand mussels are buried in the sand and are therefore located by touch, not by sight! The theory does remain of some interest, although a recent analysis of whether apostatic selection could be driving polymorphism in diurnal raptors concluded that the answer is 'no'.

Nevertheless, we must not lose sight of the fact that, in some species, polymorphism could be driven by nothing at all. This is termed 'neutral selection' and occurs when no one morph has an advantage over any another (which would probably explain the patterning of the Mediterranean sand mussels). ▷

WARWICK TARBOTON

JOHANN GROBBELAAR

Above and left *Black Sparrowhawks occur in two morphs, a pale morph (left) and a rarer dark morph (above). The amount of white on the throat of the dark morph is variable.*

TREVOR HARDAKER

FAILED EXPERIMENTS *and the Holy Grail*

Above *The jury is still out on whether a single theory can explain the benefits of polymorphism among Parasitic Jaegers.*

Below *Male Ruffs vary greatly in the head and neck plumes that they display at their leks to arriving females. The reason that this variation persists – rather than natural selection resulting in a 'perfect solution' – may be that not all females make the right choices and some mate with 'substandard males', perpetuating their genes.*

ROGER POWELL/NPL/PHOTOACCESS

Scientists are always interested in rare or unusual phenomena – and these include polymorphism – because understanding them can often provide insight into why the majority of species do something different.

In the case of polymorphism among birds, it is still not clear whether there is a unifying theory to explain its occurrence, but light conditions are favoured as being a factor. Light changes hugely over a 24-hour period: levels at midday (depending on where you are) can be three billion times brighter than under the night sky. Potentially, that's a pretty powerful agent of selection!

Given that polymorphism is controlled by genes, it could arise through what is termed mutation (a genetic 'accident'). If that accident produces an inappropriate design, it is highly unlikely that the design will persist through subsequent generations. It seems very probable, therefore, that over the years many polymorphisms have appeared that never survived. And in view of the very small proportion of the world's birds that show persistent polymorphism through the generations, it appears that most of these 'experiments' are doomed to failure.

The same can be said of most plumage abnormalities, such as albinism and schizochroism. These abnormalities, which attract more photographers than prospective mates, are typically the result of an excess or shortage of a particular pigment or the result of an abnormal diet. The outcomes of these 'experiments' too are fairly much a foregone conclusion – a dead end, literally and genetically.

Polymorphism is not confined to birds: it occurs in groups ranging from plants to brittle stars, sea anemones, fish, reptiles and mammals. And, depending on their particular field of study, scientists have proposed different mechanisms by which these polymorphisms are maintained. For example, herpetologists often point to the varying abilities of differently coloured individuals to absorb solar radiation. Those who study fish mostly wave the script of mate choice (and have done some very ingenious experiments to demonstrate that they are right).

Ornithologists have examined this particular script and rejected it (although some populations of Parasitic Jaegers do show fish-like leanings). However, the Holy Grail of a unifying theory for polymorphism still eludes them. Maybe there isn't one. On Fair Isle in the Scottish Shetlands, dark-phase male Parasitic Jaegers are favoured by sexual selection – they find mates and breed earlier and more successfully than the pale males do. Yet on the adjacent island of Foula, something quite different is going on and dark males do not have the same advantage.

But, even if the Holy Grail is in fragments, it's fun playing with the pieces! □

POLYMORPHIC SPECIES

The African bird species listed here can be described as polymorphic because colour variation between individuals is not attributable to age, sex or subspecies. It should be noted, however, that the categorisation of three species (Wahlberg's Eagle, Bat Hawk and Red-billed Quelea) as showing continuous polymorphism is problematic, as the morphs in these cases may be multiple, but also discrete.

ALBERT FRONEMAN

PETER RYAN

Booted Eagles occur in two colour morphs – pale and brown. In South Africa, as in Spain, about 80 per cent of breeding birds are the pale morph.

DISCRETE POLYMORPHISM

Southern Giant-Petrel *Macronectes giganteus*
Soft-plumaged Petrel *Pterodroma mollis*
Wedge-tailed Shearwater *Puffinus pacificus*
Red-footed Booby *Sula sula*
Western Reef Heron *Egretta gularis*
Dimorphic Egret *Egretta dimorpha*
Gabar Goshawk *Micronisus gabar*
Black Sparrowhawk *Accipiter melanoleucus*
African Goshawk *Accipiter tachiro*
Ovambo Sparrowhawk *Accipiter ovampensis*
Jackal Buzzard *Buteo rufofuscus*
Booted Eagle *Hieraaetus pennatus*
Eleonora's Falcon *Falco eleonorae*
Long-tailed Jaeger *Stercorarius longicaudus*
Jacobin Cuckoo *Clamator jacobinus*
Common Cuckoo *Cuculus canorus* (female only)
Senegal Coucal *Centropus senegalensis*
Spotted Eagle-Owl *Bubo africanus*
Malachite Kingfisher *Alcedo cristata*
Yellow-fronted Tinkerbird *Pogoniulus chrysoconus*
Brown-throated Martin *Riparia paludicola*
Icterine Warbler *Hippolais icterina*
East Coast Boubou *Lanius sublacteus*
Somali Boubou *Lanius erlangeri*
Olive Bush-Shrike *Chlorophoneus olivaceus*
Many-coloured Bush-Shrike *Chlorophoneus multicolor*
Black-fronted Bush-Shrike *Chlorophoneus nigrifrons*
Fiery-breasted Bush-Shrike *Malaconotus cruentus*

CONTINUOUS POLYMORPHISM

Bat Hawk *Macheiramphus alcinus*
European Honey Buzzard *Pernis apivorus*
Steppe Buzzard *Buteo vulpinus*
Archer's Buzzard *Buteo archeri*
Long-legged Buzzard *Buteo rufinus*
Tawny Eagle *Aquila rapax*
Wahlberg's Eagle *Aquila wahlbergi*
Ruff *Philomachus pugnax*
South Polar Skua *Catharacta maccormicki*
Pomarine Jaeger *Stercorarius pomarinus*
Parasitic Jaeger *Stercorarius parasiticus*
Levaillant's Cuckoo *Clamator levaillantii*
African Scops-Owl *Otus senegalensis*
European Scops-Owl *Otus scops*
Sokoke Scops-Owl *Otus ireneae*
São Tomé Scops-Owl *Otus hartlaubi*
Pemba Scops-Owl *Otus pembaensis*
Gillett's Lark *Calendulauda gilletti*
Mountain Wheatear *Oenanthe monticola*
African Paradise-Flycatcher *Terpsiphone viridis*
Red-bellied Paradise-Flycatcher *Terpsiphone rufiventer*
Red-billed Quelea *Quelea quelea*