# Iris colour in passerine birds: why be bright-eyed?

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**An initial survey of iris coloration in passerine birds (Aves: Passeriformes) showed that a brightly pigmented iris is much more common in southern African and Australian birds than in those from Europe, temperate North America, and Venezuela. However, the only statistical correlation reflected the distribution of particular bird families in these regions. Ten family-level groups considered to represent monophyletic taxa were then selected for a more detailed analysis, comparing iris coloration with distribution, status, taxonomy, plumage patterns, and some biological and behavioural characters for 1143 species. No pattern associating iris colour with particular traits was common to all families, but within families there were statistically significant associations with both plumage and biology. Our expectation that social behaviour would be an important predictor of iris colour was not supported, but critical information is still lacking for many species. Future studies of avian behavioural ecology should examine critically the role of iris coloration in individual species.**

## Introduction

'Few natural objects possess greater inherent conspicuousness than the vertebrate eye.'[1] Most passerine birds have a brownish iris, but brightly coloured pigments in the irides of many birds make the eye even more conspicuous.[2] However, despite descriptive information for many bird species, the functions of iris coloration are unclear.

In a stimulating account of the significance of coloration in parulid warblers, Burtt[3] noted that there are four major types of hypothesis to account for the evolution of animal coloration: (i) physical hypotheses, depending on molecular properties of the chemical pigments; (ii) visual hypotheses, relating to effects on the animal's own vision; (iii) optical hypotheses, concerning the animal's visibility to other animals, and (iv) identity hypotheses, concentrating on individual differences and their recognition. Burtt[3] examined the coloration of different feather tracts, bill and legs, but he did not discuss iris coloration.

An investigation of the morphological basis of age-related changes in iris colour in the pied starling (*Spreo bicolor*)[4] led to a wider survey of the implication of conspicuous iris colours in passerine birds. We initially compared iris coloration in passerine birds from different geographical regions, as delimited in standard handbooks. We then attempted to relate the iris colour of all members of selected families to the distribution, taxonomy and biology of the species. From the pattern of occurrence of coloured irides it may be possible to assess which group of hypotheses is best supported: (i) if iris colour is predictable from taxonomic relationships, but shows no consistent correlation with other aspects of the biology of the species, a physical (chemical) explanation would be indicated; (ii) if iris colour is best explained by the bird's head pattern, habitat and foraging methods, it may be related to visual factors; (iii) if conspicuous iris colour is correlated with conspicuous plumage, flash colours, visual courtship displays and a breeding system such as polygyny, visibility to other birds may be the most important factor; and (iv) if iris colour is associated with sexual dimorphism, visible age criteria and frequent interactions with conspecifics, it may serve primarily for individual recognition. These categories are not mutually exclusive, however, and the optical and identity hypotheses (iii) and (iv) will be particularly difficult to distinguish.

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## Methods

Initially, we compared all passerine birds, excluding vagrants, introduced species and non-breeding migrants, as listed in standard guides for five geographical regions: southern Africa,[5] Australia,[6] Canada,[7] Europe[8] and Venezuela.[9] These data were analysed using the BMDP programme 4F ($\chi^2$ statistic).

We then selected 10 representative family-level groups for detailed analysis. Wherever possible, we have used more than one source to check the eye colour of the species concerned; in the absence of detailed descriptions or photographs, we have relied on plates, on the assumption that the artist would be unlikely to depict a distinctively coloured iris unless there was evidence for it. For each species, data were encoded in categories, as described below; details of the taxonomic groups and the sources used are listed in Table 1.

(i) Taxonomic group: 'family', genus, species. The highest category corresponds to family, subfamily or tribe divisions in the classification of Sibley and Monroe. [10] We have tried to ensure that these categories represent monophyletic groups as currently understood.
(ii) Geographical region: Nearctic; Neotropical; Palearctic; Indomalayan; Australasian; Afrotropical. Birds which occur in more than one region have been assigned to the region which includes more than 50% of their breeding range.
(iii) Iris colour: brown; red; pale (including white, yellow and blue).
(iv) Eye-ring colour: no distinct eye-ring; red; yellow; white (or other colours, e.g. blue).
(v) Head pattern: head surrounding eye as dark or darker than iris; head (or eyestripe) lighter than iris.
(vi) Male plumage colour: uniform brown, black, or green; uniform white, blue, red or yellow; bicoloured; multicoloured.
(vii) Wing pattern visible in flight: present; absent.
(viii) Tail pattern visible in flight: present; absent.
(ix) Bill colour: dark; red; pale.
(x) Sexual dimorphism in plumage: sexes alike; sexes dimorphic. We initially included also characteristics of juvenile plumage, but found that there were too many 'missing data' entries owing to a lack of information for many tropical birds.
(xi) Status: resident; migrant; nomadic.
(xii) Habitat: grassland or open country; savanna or light woodland; forest; thickets and reedbeds.
(xiii) Diet: omnivorous; frugivorous; granivorous; insectivorous; nectarivorous.
(xiv) Feeding method: ground feeder; gleaner of vegetation; perched feeding; aerial sallies.
(xv) Social system: solitary; pairs; flocks; mixed-species flocks.
(xvi) Breeding system: monogamous pairs; polygynous; brood parasites; cooperative breeders. For European passerines we used Møller's[11] review of breeding systems. Ford[12] provided a table of North American passerines for which polygyny has been reported, and Brown[13] listed records of cooperative breeding worldwide.

**Table 1**. The composition of the taxonomic groups analysed, their geographical distribution, and the main sources consulted for biological and taxonomic information.

| Taxonomic group | Genera | Species | Geographical regions | References |
|---|---|---|---|---|
| Hirundinidae (swallows) | 15 | 75 | Worldwide | Turner and Rose[30] |
| Sturnini (starlings) | 29 | 114 | Afrotropical, Palearctic, Indomalayan, Australasian | Feare and Craig[56] |
| Corvini (crows) | 26 | 121 | Worldwide | Goodwin,[57] Madge and Burn[58] |
| Ploceidae (weavers) | 17 | 110 | Afrotropical, Indomalayan | Fry and Keith,[59] Craig (unpubl. data) |
| Parulini (wood-warblers) | 26 | 117 | Nearctic, Neotropical | Curson *et al.*,[60] Ehrlich *et al.*[61] |
| Icterini (American blackbirds) | 27 | 103 | Nearctic, Neotropical | Jaramillo and Burke,[62] Ridgely and Tudor[63] |
| Turdidae (thrushes) | 15 | 161 | Worldwide | Clement and Hathway[64] |
| Meliphagidae (honeyeaters) | 34 | 129 | Australasian, Indomalayan | Beehler *et al.*,[65] Pizzey,[6] Pratt *et al.*[66] |
| Nectariniidae (sunbirds) | 16 | 130 | Afrotropical, Indomalayan, Australasian, Palearctic | Cheke and Mann[67] |
| Malaconotinae (bush shrikes) | 28 | 83 | Afrotropical, Indomalayan | Harris and Franklin[68] |

(xvii) Courtship: song from concealed position; aerial display; display from exposed position; group displays. These categories can be identified for almost all species; details such as the proximity of the sexes during courtship displays are available for few tropical species.

**Table 2**. The occurrence of brightly coloured irides among passerines from different geographical regions.

| Region | Total no. families | Total no. species | Total no. genera | % with coloured iris | |
|---|---|---|---|---|---|
| | | | | Species | Genera |
| Southern Africa | 21 | 355 | 127 | 25.6 | 39.4 |
| Australia | 20 | 299 | 101 | 35.1 | 51.5 |
| Canada | 19 | 182 | 87 | 6.0 | 11.5 |
| Europe | 17 | 164 | 66 | 7.9 | 9.1 |
| Venezuela | 19 | 654 | 290 | 11.8 | 18.6 |

The data were analysed using Statistica in pairwise comparisons of iris colour with each of the categorical variables listed above, calculating both Pearson and maximum-likelihood $\chi^2$, and the Spearman rank correlation coefficient. The data proved unsuitable for log-linear modelling, since many of the possible combinations anticipated by such programmes are not in fact represented, while missing data and monotypic genera caused further problems.

## Results

### Preliminary analysis of regional passerine avifaunas

The comparison of iris coloration in all breeding passerine birds from the different geographical regions revealed striking differences in the proportion of birds with coloured irides (Table 2). However, the only consistent statistical association was with taxonomic group, at both family and generic level. There are some families such as the Dendrocolaptidae and Motacillidae, in which no species from the selected countries/regions have coloured irides, whereas there are others such as the Icteridae, Sturnidae and Ploceidae in which conspicuously coloured eyes are a common feature. Similarly genera could be categorized as those in which no species, some species, or most species had coloured irides.

### Analysis of selected taxonomic groups

An initial analysis of the whole data set (1143 species) revealed primarily that the distribution of iris colour categories differed markedly in the different taxonomic groups (Table 3). All subsequent analyses were at 'family' level. In some cases within the family unit, species were also separated by geographical region for more detailed analysis. Table 4 shows the characteristics which showed statistically significant links to iris colour ($P < 0.05$ for each of the Pearson $\chi^2$, maximum-likelihood $\chi^2$ and Spearman rank correlation coefficient); the possible biological significance of these correlations is discussed below. There was no association between 'Status' and 'Iris colour' in any of the groups, nor between 'Iris colour' and 'Courtship'. In the latter case, this was almost certainly a consequence of missing data for many species.

### *Nectariniidae* (*sunbirds*)

In this group, only 13 of 130 species had a coloured iris, and nine of these were in two Asian genera. Thus, only a taxonomic association appeared, and there is nothing to indicate that these species differ from 'typical' sunbirds in their biology.

### *Sturnini* (*starlings*)

The seven Palearctic species were combined with the Indomalayan taxa after a preliminary analysis, and the data were then examined separately for the African, Eurasian and Australasian representatives. Although 30% of the 36 Eurasian birds had head plumage paler than the iris, this was not the case for the other regions, in which only one species showed this plumage condition. All 12 Eurasian species with a patterned tail also had a coloured iris, whereas patterned tails were lacking in

**Table 3**. Distribution of iris colour categories across the family-group taxa (see Table 1), including the expected values (in italics) calculated by Statistica ($P < 0.001$ for this distribution).

| Family* | Nect | Stur | Corv | Mala | Hiru | Paru | Meli | Icte | Turd | Ploc |
|---|---|---|---|---|---|---|---|---|---|---|
| Iris dark | 117 | 25 | 74 | 32 | 73 | 116 | 111 | 71 | 147 | 48 |
| | *92.6* | *81.2* | *86.2* | *59.1* | *53.4* | *83.3* | *91.9* | *73.4* | *114.7* | *78.3* |
| Iris red | 13 | 25 | 16 | 9 | 1 | 1 | 7 | 3 | 7 | 26 |
| | *12.3* | *10.8* | *11.4* | *7.8* | *7.1* | *11.1* | *12.2* | *9.7* | *15.2* | *10.4* |
| Iris pale | 0 | 64 | 31 | 42 | 1 | 0 | 11 | 29 | 7 | 36 |
| | *25.1* | *22.0* | *23.4* | *16.1* | *14.5* | *22.6* | *24.9* | *19.9* | *31.1* | *21.3* |

*Abbreviations: Nect, Nectariniidae; Stur, Sturnidae; Corv, Corvidae; Mala, Malaconotidae; Hiru, Hirundinidae; Paru, Parulidae; Meli, Meliphagidae; Icte, Icteridae; Turd, Turdiae; Ploc, Ploceidae.

**Table 4**. Statistically significant ($P < 0.05$) links between iris coloration and other traits in the ten groups of passerine birds (see Tables 1 and 3).

| Family | Nect | Stur | Corv | Mala | Hiru | Paru | Meli | Icte | Turd | Ploc |
|---|---|---|---|---|---|---|---|---|---|---|
| Region | X | | X | X | | | | | X | |
| Eye ring | | | | X | X | | | | | |
| Head | | X | X | | | | | | X | X |
| Male | | | | X | | | | X | | |
| Wing | | | | X | | | | X | | |
| Tail | | X | | X | | | | | | |
| Bill | | X | | | X | | | X | | |
| Sexes | | X | | X | | | | X | | |
| Habitat | | | X | | X | | | X | | X |
| Diet | | | | | | | X | X | | |
| Feeding | | X | X | X | | | | X | | X |
| Social | | | | X | | | | | | X |
| Breeding | | | | | | | | | | X |

African birds and present in only one Australasian species. A pale bill was linked with a coloured iris in Eurasia, not elsewhere. Thus these features appear to be linked to taxonomic groups rather than to any biological traits. Sexual plumage dimorphism is much more common in African starlings than in other regions, and was often associated with a coloured iris (of the same colour) in both sexes. Although feeding guild and iris colour did not show a statistically significant link on a regional basis, both African and Eurasian starlings had more ground feeders with pale eyes, and more perched feeders with coloured eyes.

*Corvini* (*crows*)

The regions are again important, since coloured eyes occur primarily in certain taxonomic lineages. Coloured eyes, whether red or pale, occur primarily in birds with dark head plumage. This is likely to be a taxonomic correlation. A coloured iris is present in close to 50% of the woodland and forest corvids, but is exceptional (one species) in birds of open grassland, and thus the association of a coloured iris with feeding in the vegetation, and a dark iris with ground-feeding, is clearly closely linked to these habitat preferences.

*Malaconotinae* (*bush shrikes*)

As currently recognized, this group is predominantly African, with just four species in the Indomalayan region. Of the 83 species, 51 have a coloured iris. All nine red-eyed species lack an eye-ring, but 18 species combine a pale iris with a coloured eye-ring. The significant correlations between multicoloured plumage, patterned tails or wings and coloured eyes suggest that visibility to conspecifics may be the critical factor. The red-eyed species are all sexually dimorphic, whereas dark and pale eyes are equally common in monomorphic and dimorphic bush shrikes. Dark-eyed species are mainly ground feeders, whereas pale eyes are most common in gleaners and hawkers. Those encountered singly or in pairs tend to be dark-eyed, whereas pale eyes are commoner in species which form larger groups.

*Hirundinidae* (*swallows*)

Two congeneric swallows with coloured eye-rings and coloured bills are the only species which have distinctively coloured eyes, so this seems to be a taxonomic correlation.

*Parulini* (*wood-warblers*)

This American family includes many brightly plumaged species, often migratory, and many with distinct eye-rings. However, only one species has a red iris and thus no correlations were to be expected.

*Meliphagidae* (*honey-eaters*)

Within this large Australasian family the number of species with coloured irides is relatively small (18 of 128) and thus the apparent correlation of a coloured iris and predominantly insectivorous diet is not well supported.

*Icterini* (*icterids, American blackbirds*)

There are consistent differences in the patterns found in North America (NA) and South America (SA), suggesting that phylogeny is again an important component in the significant correlations. Male plumage is uniformly dark in all NA icterids with a coloured iris, whereas in SA a coloured iris may be found in any plumage category. There is also a significant correlation between the presence of a patterned wing and a coloured iris in NA but not in SA, although some southern species do combine these traits. Red bills (in five species) are always combined with a dark iris; in NA dark bills and a pale iris occur together, whereas in SA there is a strong correlation between pale eyes and pale-coloured bills! Most NA species are sexually dimorphic and a coloured iris occurs only in dimorphic icterids; this correlation is less marked in SA but also supported statistically. There are few forest icterids in NA, and a coloured iris is restricted to species of more open habitats, whereas in SA more than half the forest species have a coloured iris, yet this character is not found in any other habitat. Finally, all SA frugivores have a coloured iris, but otherwise there is no diet-related pattern.

*Turdidae* (*thrushes*)

The only representatives of this family with coloured eyes (14 of 161 species) are found in the Neotropical and Indomalayan regions. In both areas these species combine a dark head with a coloured iris.

*Ploceidae* (*weavers*)

In weavers with a coloured iris, the head is always darker than the iris in colour, while a dark iris is typically combined with a head that is lighter in colour. Thus, the eye is usually conspicuous. Habitat, feeding, social system and breeding in this family show strong correlations,[58] so it is not surprising that iris colour is correlated with all four traits. A coloured iris is found in all reed-bed inhabitants, most grassland weavers, and about 50% of the savanna and forest species. Eyes are commonly pale in perched feeders, red in 'gleaners', and dark in ground-feeding species. Birds usually found in pairs have a coloured iris in 50% of the species, but this proportion is larger for those weavers typically found in flocks. A pale iris predominates in polygynous species, while eight of 12 cooperative breeders have a dark iris. Without a detailed phylogeny, it remains difficult to separate an underlying taxonomic pattern from one tied to ecology or behaviour.

## Discussion

In this analysis we have assumed that iris colour is a constant feature of a particular species. However, iris coloration may vary within a population as in the bearded tit (*Panurus biarmicus*),[14] show geographical variation as in the greater blue-eared glossy starling (*Lamprotornis chalybaeus*),[15] or change seasonally as suggested for the black-bellied glossy starling (*Lamprotornis corruscus*).[16] Short-term changes also occur. Rowley[17] noted that the eye of the white-winged chough (*Corcorax melanorhamphus*) became 'engorged' and prominent during display, though he did not mention changes in colour. Black-bellied glossy starlings handled for ringing changed their eye colour from yellow to red.[18,19] In both these species, increased blood flow to the iris could account for the observed changes, and the iris is conspicuously coloured at all times. The colour of the nictitating membrane may also produce temporary changes as in the magpie (*Pica pica*),[20] and in this way a dull-coloured iris can become conspicuous temporarily. Such information is available for few species, and an obvious deficiency in our analysis was that morphological information was much more complete than biological and behavioural data.

Our descriptions of both plumage coloration and iris colour are of course from the perspective of a human observer. Birds do not necessarily see colour as we do; for instance, it has been known for some time that they have significant capacity for vision in the ultraviolet region of the spectrum.[21] However, our emphasis here is on conspicuous contrasts in colour and pattern, and changes in colour, not on the putative function of particular colours.

### Physical hypotheses

As shown by the taxonomic analysis (Table 3), closely related species often show similar iris coloration. Looking beyond the passerines, generic group is a good predictor of iris colour in waders.[22] All oystercatchers (11 species) have red or yellow irides and a coloured eye-ring, and all stone curlews (9 species) have yellow irides. Among the plovers, 21 of 24 species in the genus *Vanellus,* but only two of 31 species in the genus *Charadrius* have a red or yellow iris. The avocets and stilts are split between four dark-eyed and three red-eyed species, but for the rest only three monotypic wader genera have a red or yellow iris. In future it may be possible to plot iris colour on phylogenetic trees, but currently well-established phylogenies are not available for most of the taxonomic groups considered here.

Members of the same genus are likely to select similar habitats, and may resemble each other in behaviour and biochemical characteristics. Nevertheless, in a wide-ranging survey, including many of the taxonomic groups used in the present study, Oehme[23] found that there was little consistency in the chemistry of iris pigmentation in related species. Similarly, yellow and red irides can be produced by a variety of pigment combinations and other structural features.[24–27]

### Visual hypotheses

There is little evidence that the visible iris coloration affects the amount of light entering the eye. In all species examined so far, the posterior border of the iris is heavily pigmented with melanin and evidently opaque, while the pigments responsible for brightly coloured irides lie anterior to this tissue region.[4,23,28]

Worthy[29] speculated on a relationship between eye colour and quick versus deliberate behaviour in birds. In his analysis, dark-eyed birds tended to be quick and light-eyed birds deliberate in their flight, feeding and escape behaviour. The irides of aerial feeders such as swifts and nightjars are all dark-coloured, while the only two swallows with coloured irides are the distinctive African and Asian river martins of the genus *Pseudochelidon,* which are regarded as constituting a separate subfamily.[30] Their biology is not well known, but it appears to be similar to that of 'conventional' dark-eyed swallows. The broad feeding categories used in our analysis are not an adequate test of Worthy's proposal. However, a dark iris was correlated with ground feeding in three groups (Corvini, Malaconotinae and Ploceidae), whereas the ground-feeding Sturnini were mostly pale-eyed.

### Optical hypotheses

Since the avian iris contains predominantly striated muscle fibres under voluntary nervous control,[31] changes in pupil size can provide close-range signals during behavioural interactions. This has been reported for some corvids,[20,32,33] parrots[34] and icterids.[35] In the pied starling we have observed a dominant bird contracting the pupil, and thus displaying a larger area of white iris, as it approached a subordinate. This also occurs during food exchanges between flock members,[36] when the donor bird contracts its pupil. We suspect that such details have often been overlooked in descriptions of bird displays, since they are only apparent at very close range.

In their review of the drongos, Mayr and Vaurie[37] stated that the iris is brown in most birds, but can also be red, yellow or white, particularly in black birds such as crows and grackles. While there are some striking examples of brightly coloured irides in these groups, the present analysis does not support the idea that plumage colour is a good predictor of iris coloration. A coloured iris and a coloured eye-ring were associated in the bush shrikes, but in other groups a coloured eye-ring is most often found with a dark iris, suggesting that an eye-ring may represent an alternative method of 'highlighting' the eye region.

### Identity hypotheses

In all species with coloured irides which have been studied,[4,14,39,42,44,48,50–54] the adult iris colour differs from that of juvenile birds. The normal sequence is for juvenile birds to have a dull-coloured iris, which changes to become bright-coloured. However, in the forest weaver (*Ploceus bicolor*), Wood[38] found that the largest birds had dark brown eyes, whereas smaller birds (on weight and wing-length) had a brick-red iris. Size is presumably age-related, since there is little sexual dimorphism in size in this monogamous species.

The change in iris colour may commence early as in the bushtit (*Psaltriparus minimus*)[39] or may take several years as in the pied starling,[4] so that longevity need not be a factor. The pied starling is a cooperative breeder, in which normally only adults breed, while juveniles and subadults fill the role of helpers.[40] Other African starlings known to be cooperative breeders also have brightly coloured irides: golden-breasted starling (*Cosmopsarus regius*),[41] ashy starling (*Cosmopsarus unicolor*) (N. Baker, pers. comm.), long-tailed starling (*Lamprotornis caudatus*),[42] Rüppell's glossy starling (*L. purpuropterus*) (J. Dittami, pers. comm.), Cape glossy starling (*L. nitens*),[43] chestnut-bellied starling (*L. pulcher*),[44] superb starling (*L. superbus*),[45] Fischer's starling (*Spreo fischeri*),[46] and the yellow-billed oxpecker (*Buphagus africanus*)[47] and red-billed oxpecker (*B. erythrorhynchus*).[48] Iris colour can serve as an indicator of age classes for the human observer,[49] and may be used by birds in the same way. There is some evidence in raptors that mate selection may be influenced by age of the partner as indicated by iris colour.[50,51] However, in the highly social New World jays in the genus *Cissilopha,* there was no apparent direct relationship between the maturation of iris colour and measures of sociality.[52] We found some correlations between a coloured iris and flocking; this might be associated with threat and other displays during intra- or inter-specific competition for food.

Sexual differences in iris colour are not common, but of the groups used in this study, they are widespread in the *Ploceus* weavers, and also found among some icterids such as Brewer's blackbird (*Euphagus cyanocephalus*). The genus *Ploceus* includes both monogamous and polygynous species, and it is notable that the sexes differ in iris coloration only in the polygynous species, which are also most dimorphic in size and plumage.[53,54] Brewer's blackbird is less dimorphic than other icterids, and is also usually monogamous, although it forms large flocks and breeds in colonies.[55] There are other monogamous birds in which the sexes do not differ in plumage but are dimorphic in iris colour, such as the saddle-billed stork (*Ephippiorhynchus senegalensis*), in which the male has dark eyes and the female a bright yellow iris.[2]

## Conclusions

A brightly coloured iris contrasting with the surrounding head area may serve as a 'badge' distinguishing age classes, or as a variable signal during social interactions. Future studies of the behaviour of birds with coloured irides should investigate these possibilities, which relate to optical and identity hypotheses. Burtt[3] emphasized that 'a varied, integrative approach to the study of color is important', and evolutionary history cannot be ignored. The elucidation of the site of pigment formation and the biochemical pathways involved will also provide clues as to the evolution of iris coloration in related bird species. This analysis does not provide support for any unitary explanation of iris colour in passerines. Clearly, more detailed studies of individual species are needed to frame and test hypotheses. We hope that this overview will promote the inclusion of iris coloration as a topic for investigation in future studies.

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