LETTER

Evolutionary drivers of seasonal plumage colours: colour change by moult correlates with sexual selection, predation risk and seasonality across passerines

Abstract

Alexandra McQueen,¹* (1) Bart Kempenaers,² (1) James Dale,³ (1) Mihai Valcu,² (1) Zachary T. Emery,¹ Cody J. Dey,⁴ (1) Anne Peters¹ (1) and Kaspar Delhey¹ (1) Some birds undergo seasonal colour change by moulting twice each year, typically alternating between a cryptic, non-breeding plumage and a conspicuous, breeding plumage ('seasonal plumage colours'). We test for potential drivers of the evolution of seasonal plumage colours in all passerines (N = 5901 species, c. 60% of all birds). Seasonal plumage colours are uncommon, having appeared on multiple occasions but more frequently lost during evolution. The trait is more common in small, ground-foraging species with polygynous mating systems, no paternal care and strong sexual dichromatism, suggesting it evolved under strong sexual selection and high predation risk. Seasonal plumage colours are also more common in species predicted to have seasonal breeding schedules, such as migratory birds and those living in seasonal climates. We propose that seasonal plumage colours have evolved to resolve a trade-off between the effects of natural and sexual selection on colouration, especially in seasonal environments.

Keywords

Biannual moult, breeding plumage, colour change, crypsis, eclipse, pre-alternate, predation risk, seasonal breeding, seasonal phenotype, sexual selection.

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INTRODUCTION

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Some birds undergo seasonal colour change by moulting twice each year, typically alternating between a cryptic, non-breeding plumage and conspicuous breeding plumage ('seasonal plumage colours'; Butcher & Rohwer 1989; Fig. 1). Colour change by moult can be dramatic - for example the male red fody (Foudia madagascariensis) moults its brown head and body feathers to become intense red with a black eye-stripe (Craig 2018; Fig. 1a) - or subtle, as in male swamp sparrows (*Melospiza georgiana*), that moult the dark stripes of their crowns to plain rust and buff-coloured faces to ash grey (Rising 2018). Compared to other mechanisms of avian colour change, such as feather abrasion or the use of cosmetics (Box 1), colour change by moult is associated with substantial changes in physiology, with impacts on thermoregulation, activity levels and energetic reserves (King 1981; Lindström et al. 1993; Murphy 1996). The moult to breeding plumage takes days or weeks to achieve (Peters et al. 2013; Beltran et al. 2018) and cannot easily be reversed (but see Montgomerie et al. 2001). Consequently, colour change by moult may need to be accurately timed to environmental cues (Beltran et al. 2018; Zimova et al. 2018).

Conspicuous colours are considered advantageous for mate attraction and competition for resources; however they may also be costly if they increase detectability to predators (Andersson 1994; Huhta 2003; but see Cain *et al.* 2019). By moulting twice to change between conspicuous breeding and

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²Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard Gwinner Str, 82319 Seewiesen, cryptic, non-breeding plumages, birds may use colours to attract mates and signal their competitive ability while limiting the time they are visually exposed to predators (Butcher & Rohwer 1989). This adaptation may be especially important for species under intense sexual selection for highly conspicuous colours - as increased conspicuousness itself may increase predation risk (Huhta 2003) - as well as species that are already vulnerable to predators due to other factors, such as a small body size (Götmark & Post 1996). Consistent with this, Tökölyi et al. (2008) found a positive correlation between seasonal plumage colours and polygynous breeding in finches and allies. In addition, it has been shown that the change from conspicuous breeding to cryptic, non-breeding plumage is associated with a reduction in perceived predation risk in superb fairy-wrens (Malurus cyaneus, Fig. 1b; McQueen et al. 2017). If seasonal plumage colours have generally evolved as a result of strong sexual selection, we predict they will be more common in sexually dichromatic species with polygynous breeding systems and no paternal care (Andersson 1994; Dale et al. 2015). In addition, we expect seasonal plumage colours will be more common in small, ground foraging birds that live in open habitats, as these factors are associated with high predation risk (Cohen et al. 1993; Götmark & Post 1996; Griesser & Nystrand 2009; Martínez et al. 2018).

Seasonal plumage colours are also expected in birds with seasonal breeding schedules (Crook 1964). Seasonal breeding implies transitions between a breeding period, during which

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Figure 1 Examples of seasonal plumage colours: (a) male red fody (*Foudia madagascariensis*) and (b) male superb fairy-wren (*Malurus cyaneus*), in nonbreeding plumage, during moult and in breeding plumage (left to right). Photographs are by (a) Jacques de Speville and (b) David Nightingale (left, centre) and Kaspar Delhey (right).

individuals benefit from being conspicuous for mate attraction and competition, and a non-breeding period, when crypsis is favoured to avoid predation (Andersson 1983; Butcher & Rohwer 1989). We therefore predict that seasonal plumage colours should be more common in migratory species and species in seasonal habitats, where breeding is limited to part of the year and birds alternate between breeding and non-breeding physiology (Hau 2001; Goymann et al. 2012). By contrast, residents in environments with low climate variability often have relaxed breeding schedules (Johnson et al. 2012; Stouffer et al. 2013; González-Gómez et al. 2013) and should therefore lack seasonal plumage colours. Evidence for this has been found in African weavers: species with seasonal plumage colours live in arid environments where breeding is restricted to a short, rainy season, while species with seasonally monochromatic plumage live in humid forests with stable climates, where they are found in breeding condition most of the year (Crook 1964). Annual changes between breeding and nonbreeding physiology may also provide a proximate mechanism for the evolution of seasonal plumage colours. For example, hormones such as oestrogen, testosterone and luteinising hormone are involved in regulating both the moult to breeding plumage and changes between breeding and non-breeding states (Kimball & Ligon 1999; Peters et al. 2013; Pérez et al. 2018).

Here, we investigate the evolution of seasonal plumage colours in the largest bird radiation: the passerines (order Passeriformes, comprising c. 60% of all bird species). We assess the prevalence of seasonal plumage colours and estimate the number of times the trait has been gained and lost throughout evolutionary history. We test the hypotheses that seasonal plumage colours have evolved in response to (1) strong sexual selection, (2) high predation risk and (3) seasonal breeding schedules.

METHODS

Seasonal plumage colours

We assessed the occurrence of seasonal plumage colours for 5901 species of passerines using the Handbook of the Birds of the World ('HBW'; del Hoyo *et al.* 2018). Birds were classified as having seasonal plumage colours if they have (1) seasonal variation in colour and (2) biannual moult (i.e. birds with a distinctly coloured non-breeding and breeding plumage that is achieved by a pre-alternate and pre-basic moult; Howell *et al.* 2003; Howell 2010).

To score the presence or absence of seasonal plumage colours, we first checked the 'Morphological Aspects' description for each family; we assumed seasonal plumage colours were absent in species of families that were stated to have no seasonal variation in colour or a single annual moult (N = 32families). To assess the validity of this approach, we randomly selected 10 families (N = 502 species) where seasonal plumage colours were assumed to be absent and scored the presence or absence of the trait for males and females of each species; we found the trait was indeed absent in all cases. For the remaining families, seasonal plumage colours were scored as present or absent for males and females of each species based on the information in the species description section (N = 65 families). We also used information in the 'Morphological Aspects' section of the family description where there was species-specific moult information. We checked for descriptions of seasonal variation in colour (e.g. plumage described as breeding/non-breeding, dull/bright or nuptial/eclipse). We assumed species have a biannual moult when expressly indicated (e.g. it was stated that seasonal variation in colour was due to moult or that the species had a 'pre-alternate', 'prebreeding', 'pre-nuptial' or 'biannual' moult). In addition, we

Box 1. Within-year variation in bird colours

The focus of our study is seasonal colour change by moult ('seasonal plumage colours') however there are several other ways that birds undergo colour change. These differ according to whether they involve a distinct or continuous change and the degree to which colour change is regulated by behaviour. Some birds use multiple methods of colour change (e.g. see Crook 1964).

Seasonal colour change by moult: Most birds undergo one complete moult per year (known as 'pre-basic' moult; Howell *et al.* 2003; Howell 2010). However, for birds to undergo seasonal colour change an additional moult is required. This typically occurs as an incomplete moult prior to the breeding season (known as 'pre-alternate' moult; Howell *et al.* 2003; Howell 2010) and allows birds to alternate between a cryptic, non-breeding plumage and a relatively conspicuous, breeding plumage each year (Butcher & Rohwer 1989).

We note that many birds have a pre-alternate moult but do not undergo seasonal colour change (Howell 2010; Rodewald 2015). For example, female superb fairy-wrens undergo a similar pre-alternate moult of their anterior body plumage as male conspecifics (shown in Fig. 1b) but retain brown plumage colours year-round. A pre-alternate moult that leads to colour change is termed an 'obligate pre-alternate moult' (Howell 2010). For the purpose of this study, we refer to a seasonal change in plumage colour by a biannual (pre-basic and obligate pre-alternate) moult as 'seasonal plumage colours.'

Seasonal plumage colours involve a relatively defined colour change (i.e. an alternation between two distinctly coloured plumages). This form of colour change is not readily modified by behaviour.

Example: see Fig. 1.

Feather abrasion: Some birds have feathers that are specialised for colour change, where the surface colours abrade to reveal a different colour underneath (Tökölyi *et al.* 2008). Colour change by abrasion can be dramatic, and allow for seasonally distinct colours; however it can also be subtle, and involve a relatively continuous colour change over time (del Hoyo *et al.* 2018). Colour change by abrasion can be modified to some extent by behaviours that increase wear (Montgomerie & Lyon 2011).

Example: Snow buntings (*Plectrophenax nivalis*) abrade tan and brown feathers by actively rubbing against snow, causing their plumage to become immaculately white and black (Montgomerie & Lyon 2011).

Colour fading: Feather colours can degrade noticeably between moults due to the accumulation of dirt and fat (Delhey *et al.* 2006), feather wear (where abraded feathers are not designed to reveal a new colour underneath; Surmacki *et al.* 2011a), feather-degrading bacteria (Shawkey *et al.* 2007) and solar bleaching (Surmacki *et al.* 2011b). This form of colour change is relatively subtle and continuous (Delhey *et al.* 2010), and can be modified to some extent by preening (Zampiga *et al.* 2004).

Example: The blue plumage of the mountain bluebird (Sialia currucoides) fades noticeably over time (Surmacki et al. 2011a).

Application of cosmetics: Some birds enhance their plumage colours through the application of coloured substances, or 'cosmetics,' such as preen wax or oils secreted by the skin, powders produced by specialised feathers, and soils that are rich in ironoxide (reviewed in Delhey *et al.* 2007). Plumage dirtying may also be used to conceal bright plumage and increase crypsis, rather than enhance plumage attractiveness (Montgomerie *et al.* 2001). This form of colour change is highly flexible and modified by behaviour.

Example: Some hornbill species (genera *Buceros, Aceros, Penelopides*, and *Rhinoplax*) use oils from their preen gland to stain their plumage and casque yellow or red (Delhey *et al.* 2007).

Colour change in eyes and bare parts: Birds can undergo both rapid, short-term and gradual, long-term colour change of their bill, eyes and bare skin. This can occur due to changes in blood circulation, haemoglobin levels, nutritional status or hormonal status (Negro *et al.* 2006; Higgins *et al.* 2006).

Example: Crested caracara (*Polyborus plancus*) change bare facial skin from red to yellow via changes in haemoglobin concentration (Negro *et al.* 2006).

assumed a biannual moult occurs in species described as having an 'eclipse' plumage and in species that undergo a simultaneous change to a distinctly coloured breeding plumage and a (substantial) change in tail length, as this suggests at least some plumage is moulted when colour change occurs. The topic of our study is seasonal colour change by biannual moult (i.e. 'seasonal plumage colours'), so the trait was scored as absent for species with colour change due to fading or abrasion (e.g. species described as having 'fresh' and 'worn' plumage). Species that change colour by both moult and abrasion were scored as having seasonal plumage colours, even if the change due to moult is relatively minor.

We cross-checked the scores from the HBW using information on passerines in the Handbook of Australian, New

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Zealand and Antarctic Birds (Marchant & Higgins, 1990–2006) and The Birds of North America (Rodewald 2015). Based on information from these sources, an additional nine species were included as having the trait (for details see appendix S1 of the supporting information).

Some species (N = 109) were described as having seasonal variation in colour, but whether colour change was due to biannual moult was not evident from the HBW. In these cases, we consulted additional sources for moult information (in particular: Craig 1983; Marchant & Higgins, 1990–2006; Pyle 1997; Rodewald 2015; Clement & Rose 2015; see Table S1 for full reference list). Following this, moult information was lacking for 26 species described as having distinctly coloured breeding and non-breeding plumages. In

addition, for 13 species, seasonal colour change by moult is indicated, but the source notes that the presence of the trait requires confirmation, or else there is a disagreement for the method of colour change between sources. For our main analyses, we assumed these 39 species have seasonal plumage colours, as all but one have congeners with confirmed seasonal colour change by moult. However excluding these 39 species from our analyses does not affect the interpretation of our results (Table S2). A list of all species scored as having seasonal plumage colours, and whether biannual moult is confirmed, requires confirmation or is currently unknown (with supporting references) is available in Table S1.

We note that we have likely underestimated the prevalence of seasonal plumage colours due to limited descriptions for less well-known species. In an effort to address this, we used an index of 'research effort' (number of published papers per species between 1978 and 2008) provided by Ducatez & Lefebvre (2014) (N = 5831 passerine species). We assessed the possible effects of research bias by (i) repeating our main analyses excluding all species with zero published papers and (ii) including research effort as a co-variate in our analyses (categorised as: 0 = 0; 1 = 1-10; 2 = 11-50 and 3 = greater than 50 published papers, as we assumed the likelihood of trait detection would not differ between moderately and well-studied birds but could be underestimated for poorly studied species). Analyses excluding species with zero published papers as well as with and without research effort as a covariate yield similar results (Tables S3 - S5).

Predictors of seasonal plumage colours

Sexual selection

We used the mating system, the presence of paternal care and sexual dichromatism as three separate indices of the strength of sexual selection (Andersson 1994; Dale et al. 2015). The mating system was scored for 3484 species as: 0 = strict social monogamy, 1 = social monogamy with infrequent instances of social polygyny observed (< 5% of males), 2 = social monogamy with regular facultative social polygyny (5-20% of males), and 3 = obligate resource defence polygyny or lek polygyny (following Owens & Hartley 1998; Dale et al. 2015) using data collected from the literature (Cramp & Simmons, 1977-1994; Brown et al. 1982-2004; Marchant & Higgins, 1990-2006; del Hoyo et al. 2003-2011; Poole & Gill, 1992-2003; Dunn et al. 2001; Hockey et al. 2005; Pitcher et al. 2005; Dale et al. 2007). A small number of passerine species with polygynandrous mating systems were pooled with monogamous species (Dale et al. 2015). We note that because mating system information is based on social behaviour, the strength of sexual selection will be underestimated for socially monogamous species with high extra-pair paternity (Owens & Hartley 1998). Paternal care was scored as present or absent (N = 5809 species) following Dale *et al.* (2015) using known and inferred data provided in Cockburn (2006) as well as the HBW.

Sexual dichromatism was estimated using scanned illustrations of passerines from the HBW and the R package 'colorZapper' (Valcu & Dale 2014). We obtained RGB values for nine plumage patches (forehead, crown, nape, back, throat, upper breast, lower breast, belly and vent) for males and females of each species (N = 5809 species; for detailed methods see Delhey et al. 2019). These plumage patches were chosen as they are considered important for visual signalling and are consistently illustrated for all species (Dale et al. 2015). Sexual dichromatism scores were then computed as the mean Euclidean distances between RGB values of homologous plumage patches in males and females of the same species. Scores are based on breeding plumage for birds with seasonal variation in plumage colours and nominate species for birds with multiple subspecies. Scores were log₁₀ transformed to improve normality. The illustrations in the HBW have been used to objectively estimate colour in several comparative studies (e.g. Owens & Hartley 1998; Dey et al. 2015; Dale et al. 2015; Delhey et al. 2019) and correlate well with values obtained from plumage of museum specimens using reflectance spectrometry (Dale et al. 2015; Delhey et al. 2019).

Predation risk

We used body mass, frequency of ground-foraging and tree cover as three separate indices of predation risk. Body mass (g) data were obtained for 5875 species from the HBW, the CRC Handbook of Avian Body Masses (Dunning 2007) and from Wilman *et al.* (2014). For 391 of those species (7%), mass was estimated using the genus average. We used mean body mass when a range of values was given for the same species. Values were \log_{10} transformed to improve normality. Smaller species are thought to face higher predation risk, as they may be caught by both medium- and large-sized predators (Cohen *et al.* 1993) and have shorter lifespans, presumably due to a higher risk of extrinsic mortality (Ricklefs 2010; Valcu *et al.* 2014).

Ground foraging was computed as the percentage of foraging time spent on the ground or on water, relative to the time spent foraging elsewhere (air, understory, mid-story and canopy), using foraging data in Wilman et al. (2014) (N = 5901 species; estimated using information at the genus level for 364 species). Past research shows that predation risk is highest when foraging at ground level, possibly due to the reduced ability of prey to detect predators and because there are fewer directions to escape to in the event of an attack (Götmark & Post 1996; Carrascal & Alonso 2006; Sorato et al. 2012). Foraging on a substrate is also associated with increased responsiveness to alarm calls compared to aerial foraging, presumably because aerial foragers are better able to detect predators (Martínez & Zenil 2012). In addition, many predators prefer to search for and attack prey from above (Götmark & Post 1996; Andersson et al. 2009). By distinguishing ground foraging from foraging at different vegetation heights we are also likely to capture niche-scale differences in habitat cover (Götmark & Post 1996; Sorato et al. 2012).

We calculated the mean percentage of tree cover within each species' breeding range (N = 5809 species). Tree cover data were obtained from DeFries *et al.* (2000). Breeding ranges were estimated using data from multiple sources (Cramp & Simmons, 1977–1994; Brown *et al.* 1982–2004; Marchant & Higgins, 1990–2006; del Hoyo *et al.* 2003–2011; Ridgely & Tudor 2009) and gridded range maps (112.5 km × 112.5 km resolution) generated with the package 'RangeMapper' (Valcu *et al.* 2012). Reduced tree cover is associated with increased predation risk (Griesser & Nystrand 2009; Martínez *et al.* 2018) and we expect conspicuous plumage to be particularly risky in open habitats where birds are more easily detected by visually hunting predators.

Seasonal breeding

We used precipitation seasonality, temperature seasonality and migration status as three separate indices of seasonal breeding schedules. Temperature and precipitation data were obtained from Karger et al. (2017) and breeding ranges were estimated as for tree cover (described above). Precipitation and temperature seasonality were estimated as within-year variation in precipitation (N = 5809 species) and temperature (N = 5738 species) respectively, following Jetz & Rubenstein (2011). First, we calculated the total precipitation (mm) and mean temperature (°C) per month for all 112.5×112.5 km grid cells within each species' breeding range, using the R package 'RangeMapper' (Valcu et al. 2012); these values were aggregated to three-month averages (as three months represents a typical avian breeding period; Jetz & Rubenstein 2011). Second, we calculated the mean within-year variability for precipitation and temperature as the standard deviation between the four three-month periods per year. Finally, we defined seasonality of precipitation and temperature as the average standard deviation calculated across 35 years of data (Karger et al. 2017). Temperature seasonality was log₁₀ transformed to improve normality.

Migration was scored for 5808 species as 0 = resident, 1 = partial migration and 2 = complete migration, based on no, partial or complete separation between breeding and nonbreeding ranges respectively. Assignments were made using range maps in the HBW (Dale *et al.* 2015).

Because migratory birds do not experience seasonal changes in temperature and precipitation within their breeding range (they are absent during the non-breeding season) we assessed the effects of precipitation and temperature seasonality on seasonal plumage colours with migratory species excluded from the analysis; effects are similar as when including migratory species (Tables S4-6).

Data analyses

We used stochastic character mapping to estimate evolutionary transitions between three states: lack of seasonal plumage colours, seasonal plumage colours in males only and seasonal plumage colours in females and males (Revell 2012). This allowed us to estimate the number of times seasonal plumage colours evolved from a seasonally monochromatic ancestor, as well as transitions between male-only and female and male seasonal plumage colours. We did not estimate transitions to female-only seasonal plumage colours as this was found in only one species (this species was assigned to female and male seasonal plumage colours). Stochastic character maps were generated using the function 'make.simmap' in the R package 'phytools' (Revell 2012). To account for phylogenetic uncertainty, stochastic maps were generated for 100 phylogenetic trees (Jetz et al. 2012) and results represent an average across these. We used the 'all rates different' model ('ARD') to allow independent estimates for transitions to and from the three states. This model had a better fit than a model assuming all transitions were equally likely (equal rates, "ER" model, like-lihood ratio test: $\chi^2 = 504.3$, df = 5, P < 0.001) or a model assuming symmetrical transition rates between states ("SYM" model, likelihood ratio test: $\chi^2 = 477.7$, df = 3, P < 0.001).

We tested for possible correlates of seasonal plumage colours with phylogenetically controlled logistic regression, using the methods described in Ives & Garland (2010) and the R package 'phylolm' (Ho & Ane 2014). We considered seasonal plumage colours as a binary dependent variable (presence/absence) for each species. To account for phylogenetic uncertainty, we ran models for each analysis using 1000 different phylogenetic trees from Jetz et al. (2012). Results are therefore based on mean estimates for predictor slopes and model-averaged standard errors (Symonds & Moussalli 2011). We also report the median P value and the proportion of estimates with P < 0.05 across the sample of 1000 phylogenies. To assess the effects of each predictor alone and together with other variables we ran univariate models for each predictor and two 'full' models. The two full models include the fixed effects: sexual dichromatism, mass, ground foraging, tree cover, precipitation seasonality, temperature seasonality, migration and research effort. In addition, model 1 includes mating system (N = 3436 species) and model 2 includes paternal care (N = 5667). We used separate models for 'mating system' and 'paternal care' due to collinearity and uneven samples sizes between the two predictors (Table S7).

To assess possible sex-differences for predictors of seasonal plumage colours we ran separate univariate models for each predictor (as described above) and two response variables: (i) male-only seasonal plumage colours (i.e. species where males but not females have the trait) and (ii) female and male seasonal plumage colours (where both sexes have the trait, including the single species where only females have the trait).

RESULTS

Seasonal plumage colours are uncommon but taxonomically wide-spread among passerines: the trait is present in 4% of passerine species (243 of 5901 species) but in 22% of families (21 of 97 families; Fig. 2). Among species that are relatively well studied (those for which there is at least one published paper in 30 years; Ducatez & Lefebvre 2014) seasonal plumage colours occur in 5% (218 of 4328 species), suggesting that the presence of the trait may be underestimated. Around a quarter of species with seasonal plumage colours come from the weaver family (Ploceidae: N = 58 species). The trait also occurs in many species of cisticolas and allies (Cisticolidae), in sunbirds (Nectariniidae) and in all but one species of the whydah and indigo bird family (Viduidae; Fig. 2). Seasonal plumage colours are globally wide-spread, but less common in equatorial regions and South America (Fig. 3a and b).

Seasonal plumage colours are found in males only for 143 species and in both sexes for 99 species; just one species has female-only seasonal plumage colours (Speke's weaver, *Ploceus spekei*, though the method of colour change is not well understood for this species; Craig & Bonan 2018).



Figure 2 Phylogeny of passerine birds (N = 5901 species), showing the posterior probability of seasonal plumage colours based on 100 stochastic character maps (Revell 2012). Branch colours indicate the presence (yellow) or absence (blue) of seasonal plumage colours. Intermediate colours (red) indicate uncertainty in state reconstructions. Labels show families where seasonal plumage colours are particularly common.



Figure 3 Map of the world, showing (a) the number of species with seasonal plumage colours, (b) the proportion of all passerine species with seasonal plumage colours, (c) precipitation seasonality and (d) temperature seasonality. Map is shown in (equal area) Mollweide projection at a resolution of 112.5×112.5 km.



Figure 4 Estimated transitions between three states: the absence of seasonal plumage colours, seasonal plumage colours in males only, and seasonal plumage colours in both sexes. Estimates are averages based on stochastic character mapping carried out on a sample of 100 phylogenetic trees (Revell 2012). Directions of the arrows indicate transitions between states. Numbers and arrow thickness indicate the average number of transitions between states across all phylogenies.

Estimates from ancestral trait reconstructions suggest that seasonal plumage colours have been lost more often than gained (Figs 2 and 4). Transitions occurred from a lack of seasonal plumage colours to seasonal plumage colours in males only and to seasonal plumage colours in both sexes (Fig. 4).

Predictors of seasonal plumage colours

Analysis of seasonal plumage colours at the species level (i.e. irrespective of whether they occur in males only or in both sexes, 243 species show the trait) indicate that seasonal plumage colours are correlated with indicators of strong sexual selection; they are more common in species with polygynous mating systems, no paternal care and strong sexual dichromatism (Fig. 5a-d). High predation risk also appears to favour seasonal plumage colours, as they are more common in small and ground-foraging species (Fig. 5a, e and f), although the effect of ground-foraging is not statistically significant for one of the full models (m1). We found some evidence that seasonal plumage colours are more common in open habitats, although the effect was not apparent when controlling for other factors (Fig. 5a and g). Seasonal plumage colours are associated with predictors of seasonal breeding, being more common in migratory species and in birds from regions with strong seasonal variation in precipitation and temperature (Figs 3 and 5a, h-j). Seasonal plumage colours are positively correlated with the number of papers published per species, suggesting the trait may be underestimated in less-studied birds (Fig. 5a and k).

The effects are similar when assessing seasonal plumage colours that occur in both sexes (N = 99 species, plus one species with female-only seasonal plumage colours) and those that occur in males only (N = 143 species), although the effects of sexual dichromatism were less strong when considering seasonal plumage colours in both sexes compared to males only (Fig. S1). For details see Tables S4 and S8-10.

DISCUSSION

Seasonal plumage colours have evolved in species predicted to be under strong sexual selection and high predation risk (Fig. 5a–g). The trait is also more common in migratory birds and in species living in highly seasonal environments (Fig. 5a, h–j). Seasonal plumage colours are generally uncommon in passerines (4-5% of species), although the prevalence of the trait may be underestimated, as it is positively correlated with research effort (Fig. 5a and k).

Effects of sexual selection and predation risk

Seasonal plumage colours are associated with strong sexual selection on males (Fig. 5a-d). The trait is also more common in males than females. However, our analyses also suggest direct selection for female seasonal plumage colours, because transitions occur from male-only expression of the trait to expression in both sexes, and because seasonal plumage colours are not constrained to initially evolve in both sexes (Fig. 4; Amundsen 2000; Kraaijeveld et al. 2007). Although we did not find large differences in predictors of seasonal plumage colours for females compared to males (Fig. S1), the effect of sexual dichromatism appears stronger for male-only seasonal plumage colours. This is not surprising, since sexual dichromatism in general is an indicator of intensity of sexual selection on males (Dale et al. 2015); hence future studies should assess the effects of female-biased indices of sexual selection (e.g. Rubenstein & Lovette 2009). Strong sexual selection on males for the display of new, shiny or vibrant feathers could promote the evolution of an additional annual moult prior to breeding (Lantz & Karubian 2016) and in turn favour the evolution of seasonal plumage colours (Tökölyi et al. 2008). Selection for increasingly conspicuous plumage during breeding could also promote the evolution of seasonal plumage colours to reduce predation risk outside the breeding season.

Seasonal plumage colours are more common in small, ground foraging passerines which are particularly vulnerable to predation (Fig. 5a, e and f; Cohen et al. 1993; Götmark & Post 1996; Martínez & Zenil 2012) supporting the hypothesis that predation risk promotes the evolution of the trait. Seasonal plumage colours also tend to be found in species living in open habitats, where birds are visually exposed to predators, although the effect disappeared when controlling for other factors (Fig. 5a and g). The lack of effect of tree cover may be partly due to the coarse way in which the index was measured (average tree cover within the species breeding range), as species may select open or covered habitats within the broader landscape (Götmark & Post 1996), and even adjust their selection of microhabitat according to the degree of danger (McQueen et al. 2017; Martínez et al. 2018). High predation risk along migratory routes (Simpson et al. 2015) could also explain why seasonal plumage colours are more common in migratory species (Fig. 5a and j). More broadly, evidence for a correlation between these predictors of predation risk and seasonal plumage colours supports the widely held, but poorly supported, assertion that predation risk is an important cost of conspicuous colours in birds (see also Huhta 2003).



Figure 5 Predictors of seasonal plumage colours in passerines. Panel (a) shows model estimates based on average values from 1000 phylogenetic logistic models, each run with a different phylogenetic tree to account for phylogenetic uncertainty. Predictors were scaled and centred, error bars show 95% confidence intervals and point sizes indicate median *P* values across the 1000 phylogenetic. To test for consistency of the results, we show estimates from univariate models (each predictor separately) and from two full models (m1 and m2) designed to maximise sample sizes and include the largest number of variables in each model. Models m1 (N = 3436 species) and m2 (N = 5667 species) include the following predictors: sexual dichromatism, mass, ground foraging, tree cover, precipitation seasonality, temperature seasonality, migration and research effort; in addition, m1 includes mating system and m2 includes paternal care. Panels on the right (b–k) show the raw data comparisons between species with (Y) and without (N) seasonal plumage colours. Stacked barplots indicate the proportion of species in different categories for (b) mating system (c) paternal care (j) migration and (k) research effort. Boxplots show median and interquartile ranges for (d) sexual dichromatism, (e) body mass, (f) ground foraging, (g) percentage tree cover, as well as (h) precipitation and (i) temperature seasonality.

Effects of seasonality

Seasonal plumage colours are more common in birds that are likely to have seasonal breeding schedules, including migrants and species in habitats with strong seasonal variation in precipitation and temperature (Fig. 5a, h–j). This was expected, as seasonal breeding implies an annual change in the relative strength of selection for cryptic and conspicuous colours, where selection for conspicuous plumage is greatest during the breeding season (Andersson 1983). Crypsis to predators may also be especially favoured in winter or during the non-breeding season, when resources are scarce and an increased risk of starvation lowers the capacity of birds to maintain high levels of antipredator behaviour (Macleod *et al.* 2005; Cox *et al.* 2011). In addition, migrants and species adapted to strong temperature seasonality often moult twice to replace worn

feathers or increase plumage insulation during winter (Guallar & Figuerola 2016; Beltran *et al.* 2018). This adaptation may facilitate the secondary evolution of seasonal plumage colours (Howell 2010; Guallar & Figuerola 2016; Beltran *et al.* 2018).

Why are seasonal plumage colours uncommon?

Given the potential benefits for reduced predation risk, it is surprising that seasonal plumage colours are uncommon, having evolved on multiple occasions but subsequently more often lost (Figs 2 and 4). This has been attributed to the physiological costs of moult (Butcher & Rohwer 1989; Froehlich et al. 2005; Tökölyi et al. 2008). However there is debate surrounding the magnitude of these costs (Murphy & King 1992; Lindström et al. 1993; Murphy 1996; Ben-Hamo et al. 2017) and the pre-alternate moult to conspicuous breeding plumage often involves only a partial replacement of body plumage (Howell 2010). Although it has been suggested that proteinrich insectivorous diets may be required to meet the nutritional demands of a biannual moult (Tökölyi et al. 2008), we find no evidence for a relationship between the occurrence of seasonal plumage colours and an insectivorous diet (using data from Wilman et al. 2014). We note that seasonal plumage colours are positively correlated with omnivorous diets - which could be important for providing adequate resources to allow moult at different times of the year (Howell 2010) however the trait is also found in strictly granivorous and insectivorous species (for details see appendix S2).

We suggest seasonal plumage colours might be uncommon and frequently lost in evolutionary history because the trait requires (i) the right balance of strong sexual selection and high predation risk as well as (ii) seasonal changes in the environment that favour a defined breeding season and (iii) reliable cues that herald the arrival of ideal breeding conditions. An example for these processes is found in Malurus fairywrens. Seasonal plumage colours have been lost in two species, the lovely and white-shouldered fairy-wrens (M. amabilis and M. alboscapulatus; Fan et al. 2018). Both species have high annual survival rates (Leitão et al. 2019) and live in the tropics, where predation risk on fairy-wrens appears to be relatively low (Cain et al. 2019) and where reduced seasonality may favour less well-defined breeding schedules (Leitão et al. 2019). In purple-crowned fairy-wrens (M. coronatus), seasonal plumage colours appear to be in the process of being lost due to a lack of strong sexual selection (Kingma et al. 2009; Fan et al. 2017) and a lack of a defined breeding season, as the species can breed year-round in response to rainfall (Hidalgo Aranzamendi et al. 2019).

Conclusions and future research

Here, we show that seasonal plumage colours evolved in species that are predicted to have strong sexual selection, high predation risk and seasonal breeding. Because colour change by moult in birds is often readily detected in the field, large scale records of the timing of colour change could be used to indicate whether and how bird populations adjust their annual schedules in response to environmental change (Tulloch *et al.* 2013). It has previously been shown that mammals and birds that moult from brown to white pelage to maintain crypsis against snow have limited plasticity in response to rapid changes in the timing and duration of snow cover, resulting in low survival (Mills et al. 2013; Imperio et al. 2013; Zimova et al. 2014; Zimova et al. 2016; Atmeh et al. 2018; Mills et al. 2018). To what extent passerines have the capacity to adjust the timing of colour change in response to climate change is presently unknown, as are the consequences for sexual selection (Cockburn et al. 2009; Hau et al. 2017) and predation risk. In at least some species the timing of the moult to conspicuous breeding plumage seems flexible, and varies with environmental conditions (e.g. rainfall: Cockburn et al. 2009; van de Pol & Cockburn 2011; Fan et al. 2017). Given the multiple independent evolutionary gains of seasonal plumage colours (Fig. 2) and the diversity of underlying hormonal mechanisms that regulate the moult to breeding plumage (Kimball & Ligon 1999; Peters et al. 2013; Pérez et al. 2018), it is possible that different taxa will regulate moult timing in different ways, generating a broad diversity in plastic and evolutionary responses to change.

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AUTHORSHIP

AM, AP and KD conceived the study; AM, BK, CJD, JD, KD, MV and ZTE collected the data; AM and KD analysed the data and wrote the manuscript, with substantial contributions from all co-authors.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/ 10.26180/5d3695e37d1b2.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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