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Ecogeographical gradients in plumage coloration among Australasian songbird clades

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ABSTRACT

Aim Animal coloration often shows high degrees of evolutionary lability, producing variation among species that is easily apparent. This variation may produce consistent geographical patterns as species converge on adaptive phenotypes in similar environments. Some such geographical patterns in colour variation have been recently predicted as a response to the light environment in different habitats. Others like Gloger's rule – the negative relationship between brightness and humidity – have long been observed but still demand explanation. Finally, the conventional wisdom that tropical birds are more colourful remains largely untested.

Location Australia, New Guinea.

Methods Here, we compared plumage coloration across two families of Australian birds (Meliphagidae, $n = 97$ species; Acanthizidae, $n = 40$ species) in a combined spatial and phylogenetic framework. We assessed the extent to which environmental variables extracted from species ranges explain variation in colour traits, while correcting for the autocorrelation inherent in spatially structured data using extensive simulations.

Results We found several strong effects of environment on plumage coloration. Inland species with ranges marked by high aridity and temperature seasonality showed greater colour span among acanthizids, and greater saturation among meliphagids. Gloger's rule was supported in both clades, but more strongly for dorsal plumage. The most consistent correlate in this relationship was vegetation: birds in regions with more vegetation had markedly darker plumage. Ornament hue showed no significant associations with vegetation or climate.

Main conclusions Birds living close to the equator were not more colourful, but species inhabiting arid regions were. Species may respond to the shorter and less predictable breeding seasons of arid environments by evolving increased ornamentation. The consistent relationship we observed between vegetation and dorsal brightness supports a primary role for countershading and background matching in Gloger's rule.

Keywords

Biogeography, bird coloration, climate, comparative methods, Gloger's rule, sexual selection.

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INTRODUCTION

Understanding how organisms come to differ from one another across space is a key goal of biogeography (Lomolino et al., 2006). While simple principles of thermoregulation often underlie geographical variation in body shape and size (Bergmann, 1847; Allen, 1877), the causes of geographical patterns in animal coloration appear to be more complex. Coloration has many functions, from cryptic camouflage to seemingly extravagant visual signals. The strength and optimum of selection on each of these roles may be expected to vary spatially among habitats due to differences in breeding behaviour, climate or lighting conditions (see Théry, 2006; and also other chapters in Hill & McGraw, 2006a,b).

It is a commonly held assumption that birds in the tropics are more colourful (Wilson & Von Neumann, 1972). Previous studies have suggested that the appearance of a latitudinal gradient in elaborate coloration may be based on gradients in species richness rather than coloration (Bailey, 1978; Dalrymple et al., 2015), but the idea is remarkably persistent. Other sexually selected traits like sexual size dimorphism and sexual dichromatism appear to be at best weakly associated with latitude or climate (Badyaev & Hill, 2003; Friedman et al., 2009; Dale et al., 2015; Friedman & Remeš, 2016). In general, few studies have focused on the macroecological distribution of sexually selected traits (Dunn et al., 2001; Macías-Ordóñez et al., 2014). As such, it remains largely unclear how sexually selected traits differ spatially and in relation to climate, and thus how the selection that produces them should differ between geographical regions (Cardillo, 2002; Friedman & Remeš, 2016). While the fundamental principles that govern sexual selection may be the same in each region, the distribution of resulting phenotypes is likely to vary (Podos, 2014). Some researchers have predicted that environmental productivity should increase the density of individuals (and thus potential mates and/or competitors) and so increase the occurrence of polygyny (Verner & Willson, 1966). Alternatively, regions with highly seasonal climates may increase breeding synchrony and thus also increase the intensity of sexual selection (Emlen & Oring, 1977; overview in Friedman & Remeš, 2016). In either case we might expect to see a greater degree of elaboration in species inhabiting those regions. Studies are needed that test whether the degree of elaborate coloration of species differs with latitude, and explore which environmental variables might explain such a gradient.

Animal signals often vary in response to environmental variables that affect the medium of communication in such a manner that signal efficacy is maintained (Wilczynski & Ryan, 1999). For example, bird songs often match the acoustic properties of their habitat (Morton, 1975; Boncoraglio & Saino, 2007). Similarly, bird coloration is expected to differ between species in different habitats, as the conspicuousness of each colour varies depending on the ambient spectrum of light (Théry, 2006). While red ornaments may be particularly conspicuous in dense forests illuminated by a spectrum biased towards longer wavelengths, yellow ornaments may be more conspicuous in open deserts (Endler, 1993). Indeed, a study of Australian birds by McNaught & Owens (2002) found a significant relationship between species habitat type and both brightness and hue. Species in closed habitats were observed to have darker plumage with longer-wavelength hues.

Much of the attention to geographical variation in coloration has focused on Gloger's rule, in which animals tend to be more darkly pigmented in humid environments (Gloger, 1833). This pattern often explains considerable plumage variation among avian populations and subspecies (Zink & Remsen, 1986; VanderWerf, 2012). The potential functional explanations for this pattern have included thermoregulation, parasite defence and camouflage (Burtt, 1981; Zink & Remsen, 1986; Burtt & Ichida, 2004). While little support has materialized for thermoregulatory explanations, it remains unclear which of the other hypotheses may best explain Gloger's rule (Cowles, 1958; but see West & Packer, 2002). Few studies have explored this pattern in a modern biogeographical or phylogenetic framework, and these have largely focused on mammals (Stoner et al., 2003; Kamilar & Bradley, 2011; Santana et al., 2012). Most promisingly, Kamilar & Bradley (2011) found a relationship between dorsal pelage brightness and evapotranspiration in primates, hinting at a prominent role for crypsis.

Here we examine two diverse and closely related passerine families, the honeyeaters (Meliphagidae) and Australasian warblers (Acanthizidae), which are endemic to Australasia, a region with a great diversity of climatic regimes. Focusing on these clades allows us to test for consistent patterns in character evolution among closely related species without the added complexity of averaging across many idiosyncratic regions and clades (Gaston et al., 2008). Honeyeaters (Meliphagidae) tend to be socially monogamous and sexually monochromatic, and most rely almost exclusively on nectar or other sugary exudates. They are notoriously pugnacious defenders of these ephemeral resources, excluding even interspecific rivals (Higgins & Peter, 2001; Low, 2014). In contrast, Australasian 'warblers' and allies (Acanthizidae) are primarily insectivorous, and some exhibit year-round territoriality either in pairs or cooperatively (Hall, 1974; Higgins & Peter, 2002). In this way the feeding and breeding habits of species from both families do not easily fit to the expectations generated from ornithological research in the northern temperate zone. Moreover, past studies of elaborate coloration in birds have been aimed predominantly at the contrast between temperate North America and the Neotropics (Bailey, 1978; Macías-Ordóñez et al., 2014). Thus our model clades provide an excellent opportunity to test the generality of biogeographical rules (Blackburn & Gaston, 1998).

In this study we aimed to describe and explain the geographical variation in plumage coloration among two families of Australian bird species. We quantified the degree of elaborate coloration to test predictions of (1) a latitudinal trend in the degree of elaborate coloration, and (2) a positive

relationship to productivity and seasonality, possibly linked to sexual selection. We quantified colour characters representing the hue of ornamental plumage to (3) test predictions that ornaments are tuned to enhance conspicuousness in their light environment. Lastly, we quantified plumage brightness to (4) test predictions that high humidity or ground cover are associated with dark coloration.

METHODS

Measurements

We examined vouchered museum specimens of Meliphagidae and Acanthizidae at the Australian National Wildlife Collection (ANWC), and we include here data on all species for which both phylogenetic and spatial data were available (excluding *Pachycare flavogriseum*; Meliphagidae, 97 species out of 184 recognized; Acanthizidae, 40 species out of 64 recognized; Clements *et al.*, 2015). Due to the prevalence of sexual monochromatism in honeyeaters and thornbills, we chose to focus on the extent of male elaboration rather than doubling our sampling effort to include female plumage. We sampled five male specimens, preferentially selecting individuals in breeding condition; as breeding seasons vary considerably (Higgins & Peter, 2001), this was assessed based on skull ossification, testis enlargement and feather wear.

We used reflectance spectrometry to measure plumage coloration, employing an Avantes AvaSpec-2048 spectrometer equipped with an AvaLight-XE pulsed xenon light source. Measurements were standardized between each specimen using a WS-2 white reference, and included reflectance values for the range of 300–700 nm (i.e. including the ultraviolet portion of the spectrum). For each specimen, we measured 12 plumage patches located on the belly, breast, cheek, crown, flank, mantle, primaries, rump, tail, throat and wing coverts (Fig. S1 in the Supporting Information). We measured each patch in triplicate, then averaged and smoothed the resulting reflectance spectra in 'pavo' (Maia *et al.*, 2013). To compare these colours in the context of the avian visual system, we estimated receptor stimulus values using methods described in Vorobyev *et al.* (1998). Much of the easily observed variation in avian visual systems occurs at a single site on the *SWS1* opsin gene, some species exhibiting greater violet sensitivity (VS) and others exhibiting greater ultraviolet sensitivity (UVS; Wilkie *et al.*, 2000; Ödeen & Håstad, 2003). As honeyeaters have been described as having the VS allele (Ödeen & Håstad, 2010), we used photoreceptor sensitivities from an average VS visual system to model coloration in this study. However, interspecific variation in photoreceptor sensitivity has been observed in a closely related family, Maluridae (Ödeen *et al.*, 2012). Consequently, whenever possible we chose to use colour metrics that lacked explicit visual modelling to avoid combining plumage reflectance and receiver perception into a single character (see Friedman & Remeš, 2015). We placed each colour measurement in a colour space described by receptor stimulus values (Stoddard & Prum, 2008), but calculated additional variables describing its hue, saturation and brightness using metrics that do not explicitly model the receiver's visual system (see equations in Friedman & Remeš, 2015).

To summarize the extent of plumage elaboration across many independent body regions, we used two measures describing the average chromatic contrast among patches (colour span; Endler & Mielke, 2005) and the volume of colour space occupied by a polygon including all patches (colour volume; Stoddard & Prum, 2008). As an estimate of overall colour elaboration, these measurements have the advantage of increasing with the number and saturation of colours (e.g. a red, blue and yellow bird would be described as more colourful than a red and blue bird). However, a drawback is that elaboration is underestimated for uniformly colourful birds (e.g. a uniformly red bird would be described as equally colourful as a uniformly brown bird). To mitigate this issue, we included a second measure of overall elaboration, the degree of plumage saturation (or colour purity) averaged across all feather patches. This measure represents the ratio of the maximum to minimum reflectance values for a patch.

We calculated the hue of each species most saturated feather patch to quantify the colour of species ornaments. To describe these ornamental patches, we used Endler's segment classification method; this approach summarizes hue variation on two axes: short wavelength to mid wavelength (hereafter MS Hue), and mid wavelength to long wavelength (LM Hue). In addition, we quantified brightness for each patch as the sum of reflectance measurements in 1-nm bins across the reflectance spectrum. We averaged these values for all patches, and for dorsal and ventral patches in particular.

Spatial and phylogenetic analysis

For Acanthizidae, we used phylogenetic data from Gardner *et al.* (2010), which were inferred using maximum likelihood (ML) analysis of five mitochondrial and four autosomal loci. While not all acanthizid taxa were sampled across every locus, nearly all have data from at least one mitochondrial marker and one nuclear intron. For Meliphagidae, we used phylogenetic data from Joseph *et al.* (2014), which were inferred using ML analysis of four mitochondrial and four autosomal loci. For both ML trees, we estimated time-calibrated branch lengths using penalized likelihood analysis in 'ape' with published divergence estimates (produced in BEAST; Drummond *et al.*, 2012; Paradis, 2013).

We estimated average climate variables for each species' range using range maps available from BirdLife (BirdLife International & NatureServe, 2011) as analysed using the R package 'raster' (Hijmans, 2015). We included the following climatic and geographical variables: midpoint latitude, elevation, mean annual temperature, temperature seasonality (standard deviation × 100), mean annual precipitation, precipitation seasonality (coefficient of variation among monthly means; Hijmans *et al.*, 2005), net primary productivity (Running *et al.*, 2004) and actual evapotranspiration (Mu *et al.*, 2011). We also included data on humidity (9 a.m. average; Kriticos

et al., 2012) and an average of yearly maximum difference vegetation index (NDBI) from 1982 to 2002 (Tucker et al., 2010) As many climatic variables are correlated, we reduced their dimensionality using principal components analysis in 'vegan' (Oksanen et al., 2015). This resulted in two principal components (PCs) that included 62% of the observed variance, with positive values of PC1 representing more arid habitats with less vegetation and positive values of PC2 representing hotter lowland habitats (Fig. 1a). Phylogenetic signal was very low for climate variables ($\lambda = 0.09$), and phylogenetic correction of PCA scores had virtually no effect ($R^2 = 1.00$ compared with the uncorrected score; Revell, 2009). Despite this reduction in dimensionality, it is clear that Australasian habitats include variation beyond these axes, and it is of interest which particular climate variables best explain variation in trait values across this region. Consequently, we report results from analyses involving both the climate PCs and the individual climate variables.

To describe spatial variation in colour, we averaged these traits across species for each cell in a 0.5° grid overlaid on the Australasian region using SAM (Spatial Analysis in Macroecology; hereafter 'gridded' data; Diniz-Filho et al., 2008). We examined spatial correlations between distributions of trait values and climate variables using a spatially lagged regression model in 'spdep' (Bivand & Piras, 2015). We tested the efficacy of this approach by estimating Type I error rates using gridded data from simulated characters. We repeated the above spatial analyses using 100 characters simulated under a Brownian motion (BM) model with a rate parameter similar to those estimated from empirical data ($\sigma^2 = 0.05$; Harmon et al., 2008). We calculated the Type I error rate for each environmental predictor as the percentage of simulated characters that were significantly ($\alpha = 0.05$) correlated with it across space. These initial tests showed distressing Type I error rates (65–85%) for spatial analyses that were present even when correcting for spatial autocorrelation. This autocorrelation of ecology and historical biogeography is a common issue in macroecology (Tello & Stevens, 2012; Warren et al., 2014). To avoid the pitfalls of this issue, we conducted our primary analyses on species data in a framework that combines correction for both phylogenetic and spatial relationships (Freckleton & Jetz, 2009). Using this model, we estimated λ (the phylogenetic effect parameter) and Φ (the spatial effect parameter) for each pair of response and predictor variables (Tables S1 & S2). To mitigate any potential effects arising from the autocorrelation issues described above, we report the effect size distributions of correlations between BM-simulated characters and each predictor used in this study. These simulations indicated a more acceptable Type I error rate of 5–20% for the methods used in this study (Freckleton & Jetz, 2009), which we improve by focusing on effects that exceed the 95% confidence interval of the simulated null distribution.

We compared colour characters against each predictor variable using an R script available upon request from and kindly provided by R. Freckleton. From the resulting linear models, we calculated effect size from the standardized regression coefficient (β), as a means to assess the effect of each predictor on the trait. We considered an effect to be 'observable' if β was outside the simulated null distribution and its standard error interval did not include 0; we considered an effect to be 'strong' if β was greater than 0.5 or less than -0.5.

RESULTS

Plumage elaboration

In comparisons across meliphagid species, colour span was not related to climate to an extent greater than null expectations (i.e. all standardized regression coefficients were within the simulated distributions; Fig. 2). However, meliphagid species in arid inland regions with sparse vegetation showed greater average colour saturation (Fig. 2). This relationship was supported most confidently in relationships between saturation and precipitation and our climate PC1, but was also observed to a weaker extent for temperature seasonality, vegetation, productivity and humidity. We found no relationship between latitude and either colour span or average saturation in Meliphagidae. Gridded saturation data showed the lowest average saturation in inland Australia and the lowlands of New Guinea, and the highest saturation values in south-western Australia (Fig. S1).

In comparisons across acanthizid species, colour span was greater for species inhabiting southern lowland regions. This relationship was supported most confidently in a strong relationship between colour span and climate PC1, and relationships with latitude and elevation (Figs 1a & 2). However, we also observed weaker support for associations with precipitation, AET and climate PC2. Gridded averages of colour span had the highest values in Australia's inland grasslands, but had the lowest in the lowlands of New Guinea (Fig. S1). In contrast, average colour saturation in Acanthizidae only showed observable relationships with climate PC1, NDVI and latitude (Fig. 2).

Hue

We did not observe any relationship in either Meliphagidae or Acanthizidae between ornamental hue variables and environmental variables that exceeded null expectations (Fig. 3). We observed weak effects of several environmental predictors on meliphagid MS Hue, but these relationships were within null expectations (Figs 1b & 3). However, gridded data showed meliphagid species exhibiting redder ornamental plumage on average in the highly vegetated regions of coastal and upland Australia (Fig. S2).

Brightness

We found strong negative relationships between brightness and precipitation for both dorsal and ventral plumage patches in Meliphagidae: brighter birds live in dry regions (Figs 1c & 4). In contrast, we observed no such relationship in Acanthizidae (Fig. 4). In Meliphagidae, we observed strong effects of three environmental predictors and one of the principal components (PC1) on dorsal brightness. Meliphagid species had lighter dorsal plumage in warm
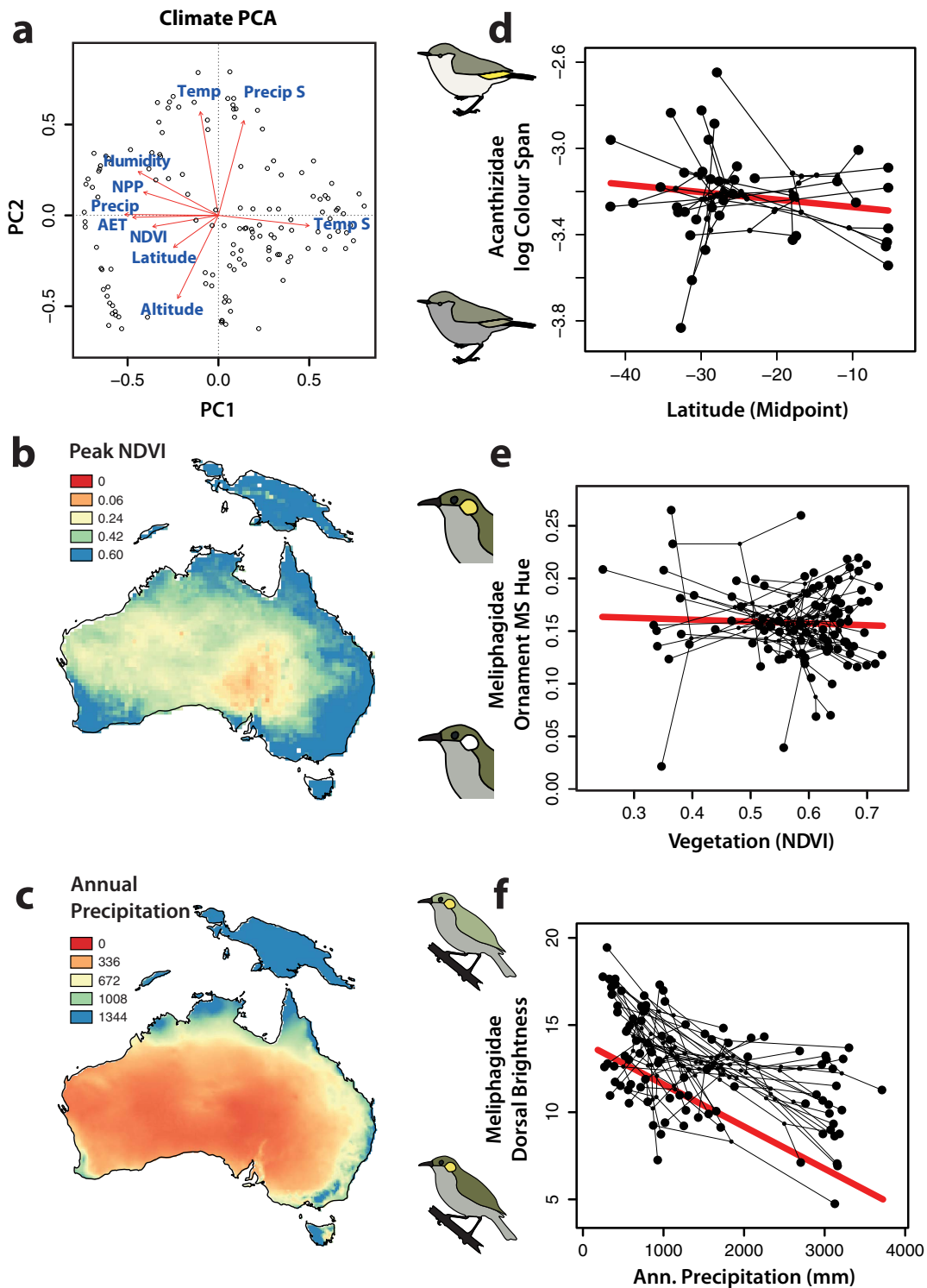
Figure 1 Results of a principal components analysis describing average climate in species ranges (a). Distribution of exemplar predictor variables across Australia and New Guinea (b, c). Plots comparing average climate and latitude of species ranges to plumage coloration (d–f). These show species trait values and climate parameters estimated from ranges (large dots), with ancestral states and relationships (small black dots and thin lines, respectively) also estimated using 'phytools' (Revell, 2012). In this context, the black lines are meant to evoke comparison of trait values among sister species and clades. Thick red lines denote regression models from analyses correcting for both phylogenetic and spatial relatedness.
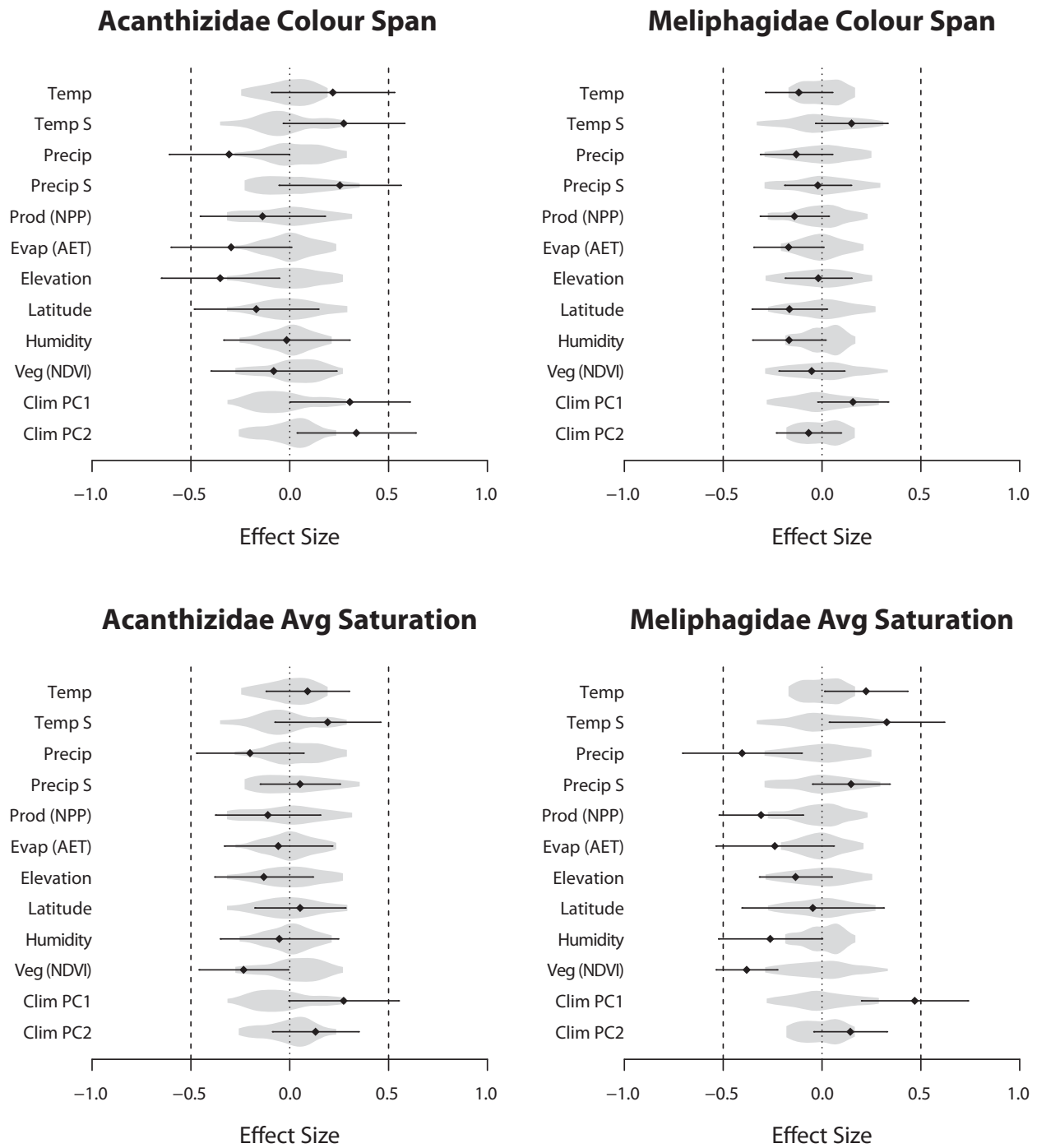
Figure 2 Forest plot of effect sizes (standardized β) and 95% confidence intervals for relationships between the predictor variables (left side) and the response variable (in bold). Null distributions estimated from correlations between each predictor and a set of 100 simulated characters are shown as grey violin plots. NDVI (Normalized Difference Vegetation Index), AET (Actual EvapoTranspiration), NPP (Net Primary Productivity), Temp S (Temperature Seasonality), Precip S (Precipitation Seasonality).

regions with high temperature seasonality, low precipitation and low evapotranspiration. We also observed these relationships in ventral plumage brightness, but they were generally weaker (but still well supported, particularly for

precipitation). In Acanthizidae, we observed a strong effect of vegetation on dorsal brightness, and a weaker effect from temperature seasonality. Climate PC1 also showed an observably positive association with both dorsal and ventral
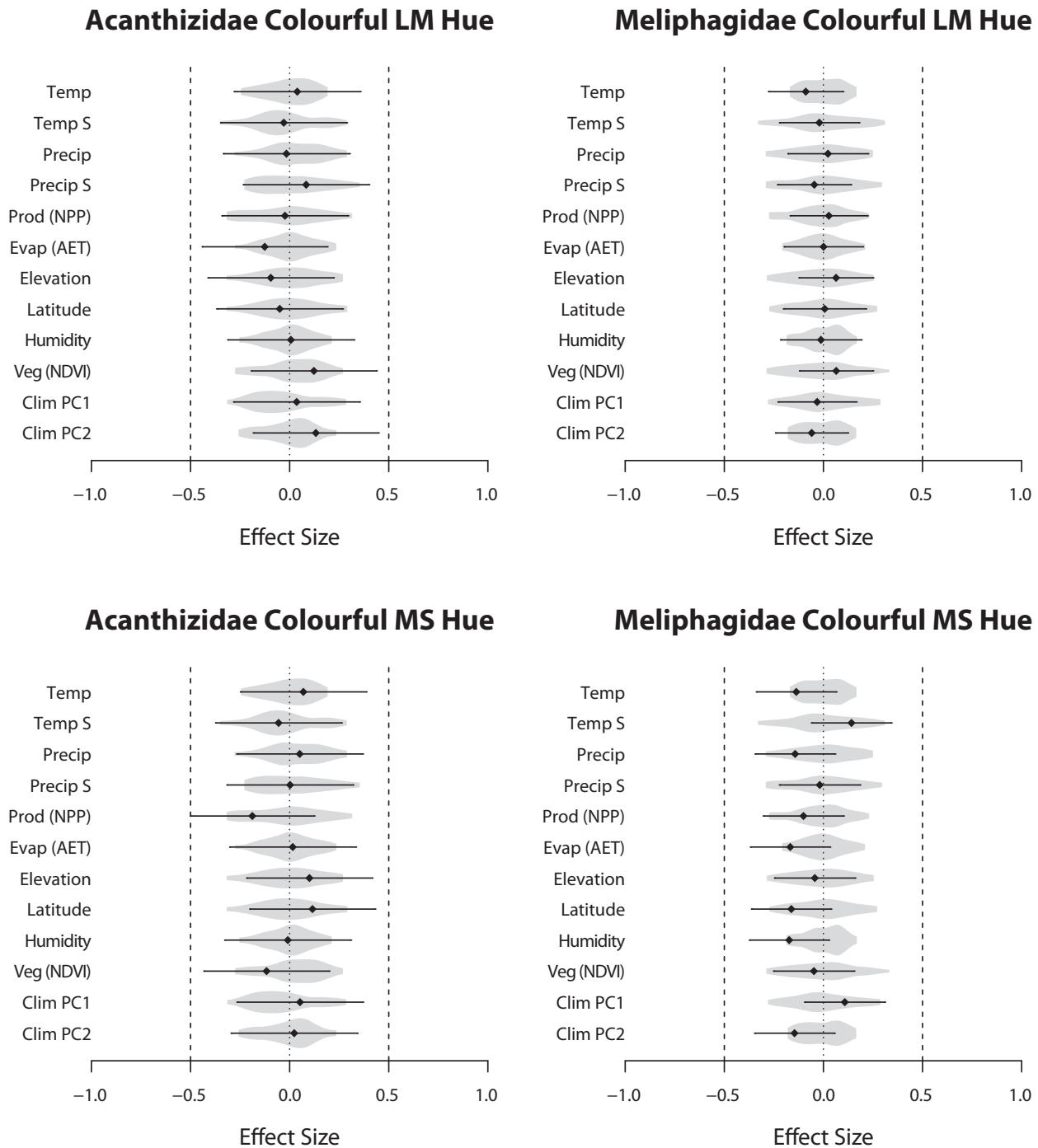
Acanthizidae Colourful LM Hue

Meliphagidae Colourful LM Hue

Acanthizidae Colourful MS Hue

Meliphagidae Colourful MS Hue

Figure 3 Forest plot of effect sizes (standardized β) and 95% confidence intervals for relationships between the predictor variables (left side) and the response variable (in bold). Null distributions estimated from correlations between each predictor and a set of 100 simulated characters are shown as grey violin plots. NDVI (Normalized Difference Vegetation Index), AET (Actual EvapoTranspiration), NPP (Net Primary Productivity), Temp S (Temperature Seasonality), Precip S (Precipitation Seasonality).

brightness. Acanthizid species had brighter dorsal and ventral plumage in arid regions with low humidity and little vegetation. Using gridded data, meliphagid species were lighter on average in Australia's inland regions, and darker in New Guinea's lowlands (Fig. S3). We observed a similar spatial pattern among acanthizid species.

DISCUSSION

Plumage elaboration, climate and sexual selection

Conventional wisdom that birds are more colourful in the tropics was not supported in this study (Fig. 2). Most studies of latitudinal variation in sexually selected traits have focused
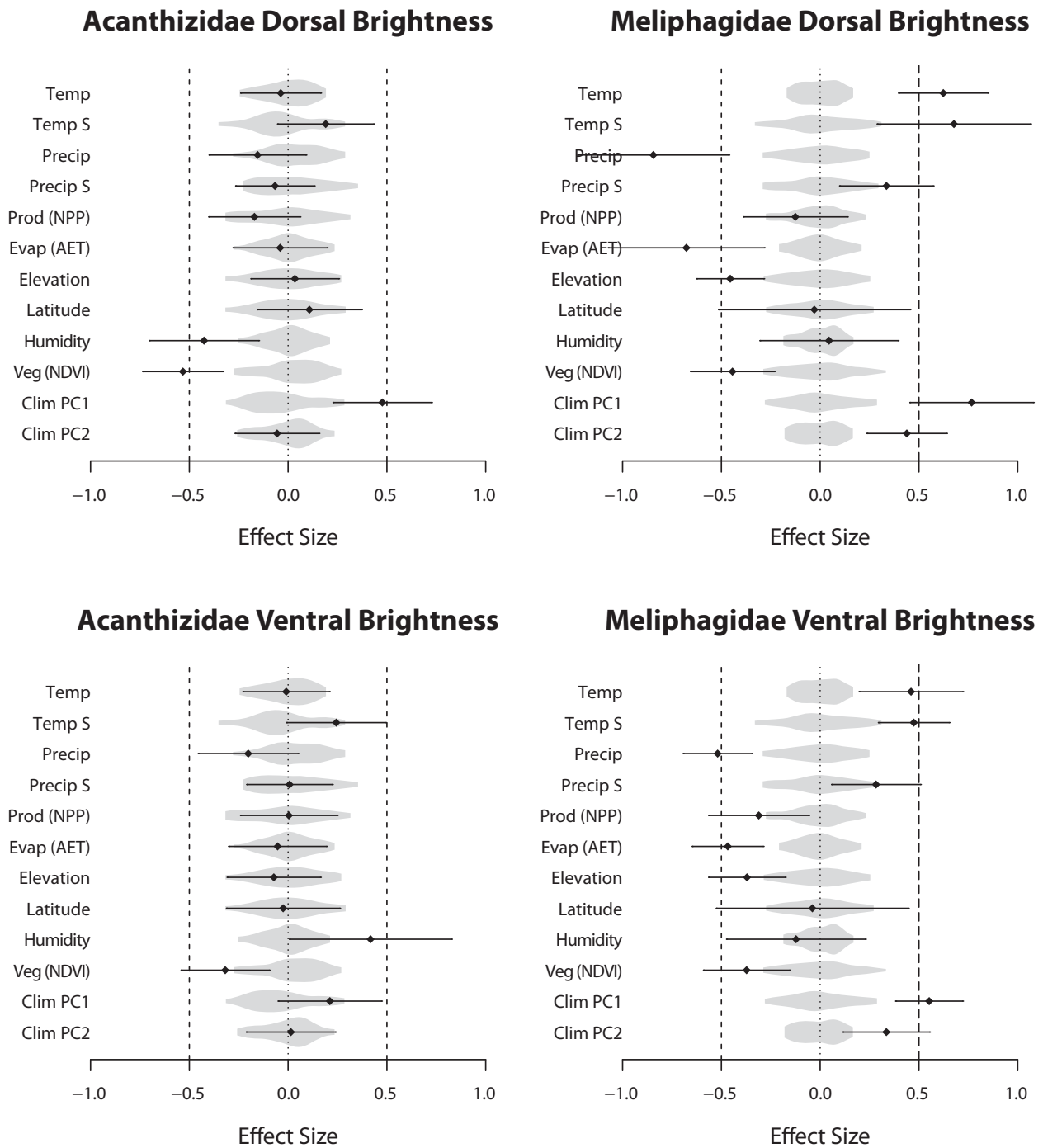
Figure 4 Forest plot of effect sizes (standardized β) and 95% confidence intervals for relationships between the predictor variables (left side) and the response variable (in bold). Null distributions estimated from correlations between each predictor and a set of 100 simulated characters are shown as grey violin plots. NDVI (Normalized Difference Vegetation Index), AET (Actual EvapoTranspiration), NPP (Net Primary Productivity), Temp S (Temperature Seasonality), Precip S (Precipitation Seasonality).

on a contrast between the Nearctic and the Neotropics (e.g. Macías-Ordóñez *et al.*, 2014). Such studies of birds are complicated by the effects of migratory behaviour and life history, which often lead to sexual dichromatism in temperate-breeding species (Bailey 1978; Friedman *et al.*, 2009). Honeyeaters and thornbills provide a unique test for an effect of latitude on

elaboration in that no species are long-distance migrants (some exhibit partial migration, diurnal or nomadic movements) and few species are sexually dichromatic (Gregory, 2016; Higgins *et al.*, 2016). In the absence of these confounding variables, there appears to be little evidence that species evolve more elaborate coloration due to conditions near the equator. If they
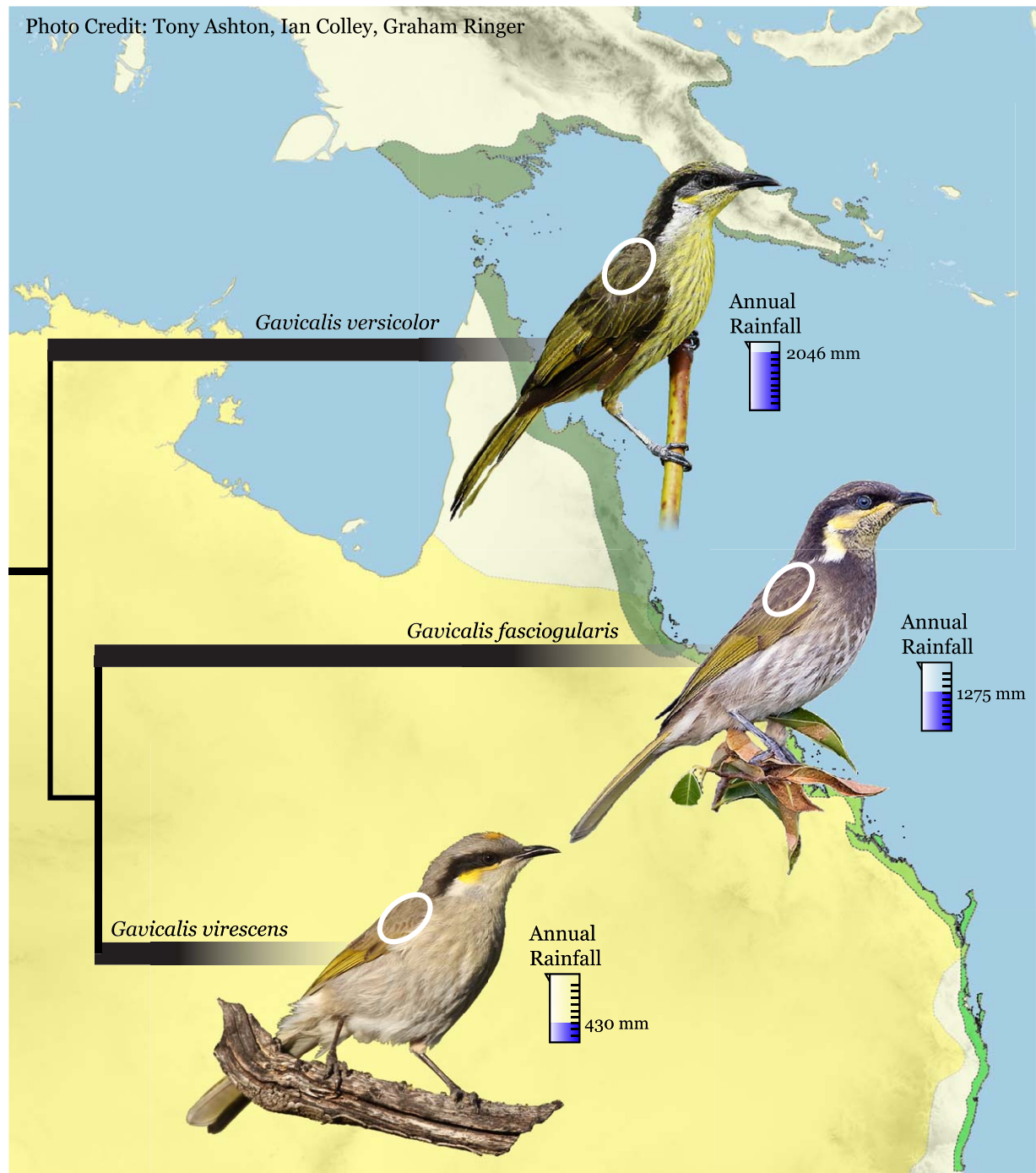
Figure 5 An illustration of Gloger's rule using the three species of the genus *Gavicalis*. Each species is shown in an example photo on the left with a single dorsal patch highlighted in white, and is overlaid onto its distributional range. Average annual rainfall for that range is indicated on the right, and phylogenetic relationships are indicated at left.

do, we should expect to see more reports of elaborate subspecies or sister taxa nearer the equator.

Instead, we found that plumage elaboration was greater for species in arid climates marked by high temperature seasonality, low precipitation and sparse vegetation (Figs 1a & 2). For meliphagids, we observed this as an increase in overall plumage saturation, whereas in acanthizids we observed this as an increase in colour span (i.e. contrast). It remains unclear why one clade should show exaggerated saturation and the other contrast, and further study of the functions of coloration in each clade is warranted. Overall, variation in these colour traits could be explained by a relationship between aridity and the intensity of sexual selection, leading to increased plumage elaboration in the arid and semi-arid zones, which show low precipitation and high variability (see Botero & Rubenstein, 2012). This could occur if breeding

events are synchronized around pulses of rainfall (McGilp, 1924; Keast & Marshall, 1954). From the highly variable climate of inland Australia, we might predict that high breeding synchrony has led to greater competition for mates and thus more elaborate plumage. While species accounts of thornbills and other acanthizids describe breeding as occurring in most months, many inland species show seasonal peaks associated with heavy rainfall (Higgins & Peter, 2002). Many honeyeaters enjoy a relatively consistent food source in the overlapping flowering periods of nectar-providing plants, but often show seasonality in their breeding that is roughly similar to acanthizids (Law et al., 2000; Higgins & Peter, 2001).

Dependence of sexually selected traits on climate variability has been reported in other Australian taxa. In superb fairy-wrens (Malurus cyaneus), more males moult into breeding plumage early and thus compete for mates in wetter years (Cockburn et al., 2008; see also Reudink et al., 2014). In arid environments with unpredictable rainfall, males must scramble to attain and display their breeding condition in time to take advantage of pulses of wet weather (Serventy & Marshall, 1957). Under these harsh conditions, elaborate plumage may be frequently gained if its condition dependence is accentuated (Cockburn et al., 2008), or if it otherwise enables individuals to make the most of the short opportunity to breed (L. Joseph, pers. comm.). It is worthy of note that many of the colourful patches observed on arid-adapted species have colours typically associated with carotenoid pigmentation mechanisms that have often been implicated in condition-dependent signalling systems (e.g. Epthianura spp.; Hill & McGraw, 2006a). Observational studies are needed to investigate the role of climate variability in species breeding behaviour and its consequences for sexual selection, particularly among arid and semi-arid endemics (e.g. Keast, 1968). If there is greater variation in mating success among species with opportunistic breeding cycles, we predict that comparative studies in other clades should also show variation in ornamentation along a gradient in aridity rather than latitude.

Hue and light environment

In a landmark paper, Endler (1993) showed that the ambient light environment differs between open and canopied habitats, and predicted that forest understorey species would be most conspicuous when adorned with red or orange colours. Since then, many studies have examined the role of the light environment in shaping avian display behaviours (Endler & Thery, 1996; Uy & Endler, 2004; Gomez & Théry, 2007). Among these, McNaught & Owens (2002) examined the hypothesis of an influence of light environment on the plumage of Australian species. They found a greater frequency of colourful (i.e. hue; sensu Endler, 1990) birds in closed habitats, but a greater frequency of bright birds in open habitats. Here we focus on colour span (i.e. contrast), but describe a similar pattern of higher average span and saturation in the semi-arid zone where open habitats are more common. In most cases, inland acanthizids achieved greater contrast by exhibiting bright yellow plumage (with the conspicuous exception of the redthroat, Pyrrholaemus brunneus). However, these colourful patches were not red or orange in forest-dwelling acanthizids, but absent altogether (Higgins & Peter, 2002). This suggests that differences exist in the degree of elaboration, and not the colour, of visual signals in Acanthizidae.

Our results do not lend support to the hypothesis that ornament colour evolves to match the optimum for the habitat's light environment. However, our study has several limitations that prevent us from rejecting this hypothesis. First, we assume that light environment correlates with forest cover. As Endler (1993) describes, there should be considerable variation in ambient light among the different microhabitats of a single forest. Indeed, some birds take advantage of this variation by displaying preferentially under favourable lighting conditions (Endler & Thery, 1996; Uy & Endler, 2004). However, it is worth noting that much of this variation in lighting conditions should be absent in inland grassland or desert habitats. To adequately test the light environment hypothesis, comparative studies are needed that relate plumage coloration to measurements of background colours and ambient light spectra for each species (e.g. Delhey et al., 2013). It is unclear whether (1) there have been few such attempts to test this hypothesis due to the practical difficulties of comparing the conspicuousness of birds' coloration in the context of a heterogeneous light environment, or (2) the results of such tests are frequently negative (e.g. Shultz & Burns, 2013) and thus under-reported. Meta-analyses are needed to assess the weight of evidence for the role of the light environment in driving the evolution of visual signals in terrestrial organisms.

Gloger's rule: precipitation or ground cover?

The presence of a relationship between climate and animal coloration is well established; however, the process underlying this pattern is less clear. In its original conception, humidity was identified as the driver of geographical gradients in plumage brightness (Gloger, 1833). In this study, we found no evidence for a negative relationship between humidity and plumage brightness. Humidity had no measurable effect on plumage brightness in Meliphagidae, and a positive effect on brightness in Acanthizidae only for ventral plumage. In contrast, precipitation showed a strongly negative effect on brightness in Meliphagidae: brighter birds live in arid regions (Fig. 4; Fig. 5). We interpret this to suggest that precipitation plays a greater role than humidity in defining the climate–brightness gradient observed among animals. We observed that among acanthizids, vegetation was the strongest predictor of a species' plumage brightness (Fig. 4). Furthermore, acanthizids often live in riparian habitats, which may vary in vegetation on a smaller scale than was measured in this study. Consequently, we find it plausible that the role of precipitation and humidity here may be in

controlling the extent of vegetation, and indeed these variables are typically correlated (Nightingale & Phinn, 2003). Future studies should employ phylogenetic path analysis methods to further disentangle the effects of these variables (von Hardenberg & Gonzalez-Voyer, 2013).

As discussed by Zink & Remsen (1986), the more marked relationship with climate for dorsal versus ventral plumage is a challenge for precipitation-related explanations for Gloger's rule. Whether mediated by parasite abundance or other factors, precipitation-related mechanisms for Gloger's rule must explain why this effect is greater in dorsal plumage. We propose two such explanations here.

1. Countershading is extremely common among animals, and mechanisms for maintaining it are deeply embedded in vertebrates' genetic architecture for melanin biosynthesis (Hoekstra, 2006; Manceau et al., 2011). Thus, selection for darker or lighter coloration may act most readily on alleles that more greatly affect dorsal coloration, whether such selection is the result of predation or precipitation. Alternatively, continued selection for countershading could maintain the difference in brightness between dorsal and ventral patches, either as a means of reducing self-shadowing or otherwise contributing to camouflage (see Ruxton et al., 2004; Rowland, 2009; Kamilar, 2009).

2. Ventral feather patches may be more often involved in signalling functions, in part because they can be more easily hidden from predators (Gomez & Théry, 2007). This would add more noise to relationships between climate and ventral plumage than dorsal plumage (e.g. if ventral plumage varies between conspicuous colours that differ in brightness). Among Australian fairy-wrens and grasswrens (Maluridae), plumage brightness evolves most rapidly on ventral feather patches for females but on ventral and some dorsal patches for males (Friedman & Remeš, 2015). This may suggest that ventral patches are under weaker selection for background matching, and are thus free to vary. Alternatively, natural and sexual selection pressures may be variable, leading to different colour optima among species. In either case, there remains a strong role for background matching in the maintenance of Gloger's rule.

CONCLUSIONS

As in Dalrymple et al. (2015), we found no support for a positive relationship between plumage elaboration and latitude: birds were not more colourful in the tropics. However, we did find evidence that meliphagids and acanthizids inhabiting arid regions had more contrasting and more saturated plumage, respectively (Fig. 2). We also found no evidence that species ornaments were tuned to different hues in different habitats (Fig. 3). Lastly, we observed strong evidence in support of Gloger's rule, highlighting the role of precipitation and/or vegetation in animal coloration.

By averaging species data across local assemblages (grid cells), we found many spatial distributions that imply relationships between species traits and their local environment, but also a Type I error rate approaching 80%. This suggests that for any particular clade it may be quite common to observe spatial trait–environment relationships. These are readily produced due to spatial and phylogenetic autocorrelation, and as such do not necessarily represent convergent adaptation to similar environments. Comparative methods that correct for phylogeny and space together with comparison against null expectations allowed us to test for correlated evolution between species plumage traits and their environment (Freckleton & Jetz, 2009). However, methods are needed to disentangle the effects of niche conservatism and historical biogeography from spatial relationships between traits and the environment.

Our results suggest that selection for elaborate coloration may be greater in arid regions. Further studies are needed that examine how different climate regimes affect the strength and direction of sexual selection. While researchers are dismantling the temperate zone bias that has afflicted behavioural ecology (Macías-Ordóñez et al., 2014), the temperate/tropical duality is likely to be an over-simplification. We can learn a great deal from Australia's arid and semi-arid zones, which have existed for millions of years as a cradle of biodiversity and crucible of evolution (Byrne et al., 2008).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1 Illustration of feather patch locations measured in this study.
Figure S2 Chloropleth maps of gridded data for measures of overall ornamentation in Acanthizidae and Meliphagidae.
Figure S3 Chloropleth maps of gridded data for measures of ornamental patch hue in Acanthizidae and Meliphagidae.
Figure S4 Chloropleth maps of gridded data for measures of plumage brightness in Acanthizidae and Meliphagidae.
Table S1 Jointly estimated phylogenetic and spatial correction parameters for phylogenetic least squares models comparing colour variables with environmental variables.
Table S2 Maximum likelihood values for phylogenetic and spatial signal parameters optimized simultaneously for response and predictor variables.

BIOSKETCHES

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