



Plumage colouration in gulls responds to their non-breeding climatic niche

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Abstract

Aim: Global variation in animal colouration has inspired ecogeographical rules that suggest common patterns of recurrent adaptations to climate. However, little attention has been paid to the relative influence of the different climatic conditions encountered by species during their annual life cycle. We explored this question by testing whether breeding or non-breeding climatic conditions most influence plumage colouration in gulls, a cosmopolitan group of birds with extensive variation in plumage darkness and seasonal migratory strategies.

Location: Global.

Time period: Contemporary.

Major taxa studied: All species and subspecies of gulls (Aves, Laridae).

Methods: We used literature data and digital images to assess two characteristics of plumage colouration in all 80 species and subspecies of gulls: the darkness of the mantle and the proportion of black on wingtips. For each species and subspecies, we collected data on migration distance and environmental variables across its breeding and non-breeding range for both breeding and non-breeding seasons. We performed a phylogenetic comparative analysis to quantify the relative influence of climatic conditions experienced during the breeding and non-breeding season on plumage colouration.

Results: The climatic conditions encountered during the non-breeding season explained interspecific variation in colouration better than the climate experienced during the breeding season. In accordance with hypotheses on the role of dark colouration in thermoregulation and feather protection, darker mantle colouration was positively correlated with insolation and negatively with air temperature. The proportion of black on wingtips was greater for long distance migrants wintering under insolated conditions than short distance migrants or residents occupying less insolated regions.

Main conclusions: In gulls, plumage colouration is predominantly shaped by selection experienced outside the breeding period, in accordance with the hypothesized photoprotective and thermoregulatory functions of avian plumage. This highlights the importance of taking into account seasonality and migration to understand global spatial patterns of avian colouration.

KEYWORDS

biogeography, bird colouration, Bogert's rule, Gloger's rule, migration distance, photoprotection, thermoregulation

1 | INTRODUCTION

Understanding the diversity and spatial distribution of animal colouration is a long-lasting puzzle in ecology and biogeography (Hill & McGraw, 2006; Lomolino, Riddle, & Brown, 2006). Large-scale variations in colouration have long been studied by evolutionary biologists and formalized as sometimes contradictory ecogeographical rules (Gaston, Chown, & Evans, 2008). For example, Gloger's rule, one of the most studied rule in colour research (Delhey, 2019; Gloger, 1833; Rensch, 1929), predicts that animals should be darker in warm and humid areas compared to colder and drier ones (Delhey, 2019; Rensch, 1929). Gloger's rule is supported by evidence from different groups of animals (e.g., Delhey, 2018; Lai, Shiroishi, Moriwaki, Motokawa, & Yu, 2008; Miller, Leighton, Freeman, Lees, & Ligon, 2019; but see Delhey, 2019) but is not fully understood yet. As recently reviewed by Delhey (2019), the proposed mechanisms explaining Gloger's rule are varied, 'including camouflage, protection against parasites, protection against solar radiation, or pleiotropic effects'. Moreover, several opposite results (i.e., darker animals found in colder regions) have recently emerged, mostly based on comparative analyses conducted on large bird families (Delhey, Dale, Valcu, & Kempenaers, 2019; Friedman & Remeš, 2017). These results are consistent with another ecogeographical rule, known as the thermal melanism hypothesis (also called Bogert's rule; Bogert, 1949), which stipulates that darker animals should be more frequent in colder regions because dark colouration absorbs more solar radiation (i.e., thermoregulatory function; Clusella Trullas, van Wyk, & Spotila, 2007; Gaston et al., 2008). Although neither Gloger's nor Bogert's rule alone offers a comprehensive explanation for the global distribution of animal colouration, it is now well established that variations of colouration are partly determined by climatic conditions.

In birds, numerous studies support the effects of climate on the evolution of plumage colouration, both at the species level (e.g., Roulin, Wink, & Salamin, 2009) and above the species level (e.g., Delhey et al., 2019). However, a comprehensive understanding of how bird colouration responds to climate remains challenging because plumage has several functions and thus experiences multiple and sometimes conflicting selective forces (Cuthill et al., 2017). Plumage colouration can be selected for social signalling (e.g., intra-specific communication, sexual attractiveness; Cuthill et al., 2017; Hill & McGraw, 2006), camouflage against predators or prey (e.g., Roulin, 2004; Zink & Remsen, 1986) or protection against parasites (Burt & Ichida, 2004; Delhey, 2019). Body colouration can also influence thermoregulation, with dark species living in cold environments being able to heat up more easily compared to light species (see Delhey, 2018; Galván, Rodríguez-Martínez, & Carrascal, 2018). Likewise, since ultraviolet (UV) radiation breaks down the molecular

structure of feather keratin, dark pigments provide photoprotection against UV radiation, thereby increasing feather resistance for species living in geographical areas with high levels of insolation (e.g., Bonser, 1995). However, dark pigments may also prevent birds from colonizing hot environments (Delhey, 2018; Friedman & Remeš, 2017; Galván et al., 2018).

An additional complication to studying the link between bird colouration and climate is that the relative importance of these functions varies with species annual life cycles and, for species inhabiting seasonal environments, with the seasonal climatic conditions. Indeed, birds may encounter different environmental conditions (i.e., seasonality) between breeding and non-breeding periods (Delhey, 2018). Non-migratory birds living in a seasonal environment experience varied climatic conditions, while migratory species may winter under climatic conditions either similar (the so called 'niche tracking behaviour'), or different ('niche switching behaviour') from those of their breeding range (see Dufour et al., 2020). Understanding which function(s) and selective pressure(s) dominate during a given period is thus even more complex for those migratory birds that travel long distance and visit multiple regions during their seasonal cycle. In summary, the selective pressures influencing plumage colouration are complex and vary throughout the annual cycle. Some bird species respond to this variation by changing plumage colouration during their annual cycles while others retain largely identical colouration all year round. For the latter species, plumage colouration may thus result from the action of multiple selective pressures acting during different periods of their annual cycle.

Understanding how the multiple functions of bird colouration combine and vary with seasonal climatic conditions remains largely unexplored. To our knowledge, all previous studies of bird colouration have explained the distribution of different colours based on the environmental conditions encountered in breeding ranges, either all year round (e.g., Delhey et al., 2019) or during the breeding period only (Galván et al., 2018). The first option would be reasonable for sedentary species that do not change plumage over the year and the second one would be appropriate for species exhibiting a seasonal colour change (see McQueen et al., 2019). However, for species that do not exhibit seasonal colour change, considering the conditions encountered only during the breeding period (for sedentary species) or only in breeding areas (for migratory species) will likely lead to overlooking some selective pressures that can be exerted on plumage colour.

Gulls (members of the family Laridae) are a large clade of birds that includes approximately 52 extant species, distributed throughout the world from the Arctic to the Antarctic, and living in open habitats always close to water bodies, whether seaside or inland (Burger, Gochfeld, & Bonan, 2019). Gulls also show a large variation in migration strategies: while some species are long-distance migrants (e.g.,

Stenhouse, Egevang, & Phillips, 2012), others occupy either high latitudes or tropical latitudes all year round (e.g., Burger, Gochfeld, Kirwan, & Garcia, 2019; Gilg et al., 2010). Gulls generally have very different plumages between the first age class and adulthood. At adulthood, their plumage remains mostly similar all year round except for head colouration, with many species developing a dark hood in breeding plumage while others acquire a variable amount of head streaking in non-breeding plumage (Minias & Janiszewski, 2020, see also Howell & Dunn, 2007; Olsen, 2018 and the Discussion section). Most gulls have reasonably similar adult plumage that mostly differs by the grey shade of the upperparts (mantle colour hereafter, ranging from white to almost black) and the proportion of black on wingtips (from no black to a complete black outer wing; Olsen, 2018) while the underparts are white in most species. In the specialized gull literature (e.g., Olsen, 2018), 'mantle colour' refers to the colour of most upperparts such as the mantle, secondaries, tertials, scapulars and wing coverts, which all have the same colour in most gull species (with a few exceptions such as *Xema sabini*). Thus, the variation in mantle colour and the proportion of black on wingtips together capture most of the variation in upperpart colouration in gulls, while underparts are white in most species (see Figure 1).

The absence of sexual dichromatism and seasonal variation of these characteristics suggests that the mantle colour and proportion of black on wingtips are not under sexual selection (Skékely, Freckleton, & Reynolds, 2004). Their predominantly top-predator position in trophic networks suggests that the back colouration of adults does not experience selective pressures to escape predators as in many other bird species. Moreover, it is assumed that the mantle colour might have a thermoregulatory function as well as a protective role against solar radiation (see Bonser, 1995; Galván et al., 2018; Lustick, Battersby, & Kelty, 1978). While the study of Gay et al. (2009) suggested that the mantle colour of some gull taxa

(*Larus occidentalis* and *Larus cachinnans*) may follow Gloger's rule at the intraspecific level, another study by Bergman (1982) further suggested that a large proportion of black on the outer wing in *Larus fuscus fuscus* (compared to closely related species) is an adaptation to overwinter in sunny, tropical climates and to migrating over long-distance. Feathers with melanin have a thicker keratin layer compared to non-melanic feathers, which confers resistance to both UV radiation and mechanical abrasion (see Bonser, 1995; Borgudd, 2003; Voitkevitch, 1966). The marked variation of grey shades, in proportion of black on wingtips and in migration strategies, combined with the limited number of functions of plumage colouration in gulls thus provide a good opportunity to address the influence of climate on animal colouration in seasonal environments.

In this study, we use gulls to investigate how the different climatic conditions encountered in the breeding and non-breeding parts of the annual cycle influence the variation of avian plumage colouration. Intraspecific variation in gulls is sometimes strongly marked, so we aimed at taking into account all observed variability by collecting colour data in all species and subspecies, representing 80 taxa in total. We quantified the migratory behaviour of each taxon (subspecies or monotypic species), using maps of their breeding and non-breeding ranges, along with georeferenced environmental variables to describe climatic conditions experienced during their breeding and non-breeding periods. In order to reduce the number of models and explanatory variables, we tested biologically meaningful hypotheses on the basis of existing literature. If mantle colour has thermoregulation and/or photoprotective functions, we expected a link between mantle colouration and temperature and insolation. If black pigment on primaries increases their resistance, we expect a link between the amount of black on wingtips and migration distance and insolation encountered throughout the seasonal cycle. We used phylogenetic comparative analyses to test whether breeding or non-breeding climatic conditions best explain the variation of these two colour traits.



FIGURE 1 Lesser black-backed gull (*Larus fuscus graelsii*) in flight. Most of the upperparts (mantle, secondaries, tertials, scapulars and wing coverts) have the same grey colour, defined as *mantle colour* in this study. The yellow polygon delineates the outer wing area (the 10 primary feathers, greater and lesser primary coverts and alula) considered to measure the proportion of black on wingtip. Photo Daniele Occhiato [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Species data

We broadly adopted the taxonomy of BirdLife International and the Handbook of the Birds of the World (HBW; del Hoyo & Collar, 2014) where gulls are treated as the subfamily Larinae. We included all species and subspecies recognized by del Hoyo and Collar (2014) but made a few taxonomic modifications (see below). This represents 80 subspecies belonging to 52 species from the genera *Creagrus*, *Rhodostethia*, *Pagophila*, *Xema*, *Rissa*, *Hydrocoleus*, *Saundersilarus* and *Larus*. Distribution data were collected from BirdLife International and HBW (2018) and gridded at a 10-min resolution. Such a high spatial resolution was necessary to analyse the distribution of taxa with narrow and fragmented breeding ranges, such as many insular species. For species having two or more subspecies, we built distribution maps of each subspecies by cropping the original species map, following

the textual information on subspecies distribution provided by Olsen (2018) and del Hoyo, Elliott, Sargatal, Christie, and de Juana (2019). We thus produced a total of 80 different rasters (see Supporting Information Appendix S4) depicting for each taxon its breeding distribution (either the breeding area for migratory species or the residence area for non-migratory species) and its wintering distribution (either non-breeding or resident area). Each taxon was categorized according to its migration strategy as *strict migrant*, *partial migrant* or *resident* (Rappole, 2013) based on information provided by reference handbooks (del Hoyo et al., 2019). For each migratory taxon (*strict* and *partial migrant*), we estimated the median migration distance by randomly selecting 5,000 points within the breeding distribution and 5,000 points within the wintering range, calculating the distance between every possible pair of breeding and wintering points and retaining the median value of these 25×10^6 distances. We applied the same method to non-migratory taxa (*resident*) with the goal to quantify potential movements within their residence area. Indeed, even if they do not migrate from one location to another, gulls often exhibit large dispersal movements throughout their range during the non-breeding season (Burger et al., 2019), and we assumed that such movements could have consequences on the abrasion of flight feathers and therefore on the proportion of black on wingtips (see Bergman, 1982). Our method thus implies a positive relationship between range size and seasonal movements for these taxa, which remains to be tested. However, we think that this approach is more realistic than considering no movement at all for sedentary taxa.

Phylogenetic relationships of gulls have been the subject of much debate (e.g., Liebers, De Knijff, & Helbig, 2004). Today, there is still no consensus about relationships between 'large gull' species, mainly because of recurrent hybridizations between taxa of very recent origin (e.g., Pons, Sonsthagen, Dove, & Crochet, 2014; Sonsthagen et al., 2016). We downloaded from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) a sample of 500 phylogenetic trees with the Hackett backbone including 51 out of our 52 recognized species. Missing species and subspecies were added according to recent taxonomic studies (e.g., Liebers & Helbig, 2002; Pons, Hassanin, & Crochet, 2005; Sternkopf, 2010; Sonsthagen et al., 2016). For every topology, we added subspecies to species terminal branches as unresolved polytomies. To assign branch length for subspecies, we extracted for each topology the terminal edge lengths of all tips and the minimal value of the most recent divergence episode (mean across topologies: 55,000 years). We used half of this value as terminal branch length for adding genetically differentiated subspecies on each topology. For other subspecies, the divergence time between subspecies was set to 10,000 years (which roughly corresponds to the end of the Last Glacial Maximum episode; Clark et al., 2009). Topologies that did not support our infra-specific relationships (i.e., branch lengths too short) were discarded (6%). Hence, we eventually considered 470 different tree topologies in our analyses. A detailed description of methods can be found in Supporting Information Appendix S2. All steps were performed with the R packages *ape* (Paradis & Schliep, 2018; R Core Team, 2019) and *phytools* (Revell, 2012). A maximum clade credibility (MCC) tree

was also computed from all topologies with the *phangorn* package (Schliep, 2011; see Figure 2a).

2.2 | Plumage colour scoring

In this study, we focused on the colouration of adult birds. Immature plumage takes between 3 and 5 years to gradually transform into adult plumage, and is highly variable between individuals within species (Olsen, 2018). Moreover, for a given species immatures can have different dispersal and migratory strategies. For these reasons, we did not address the case of immature plumage in this study (but see the Discussion section dedicated to this issue). To characterize the shade of mantle colouration in adult gulls, the standard procedure compares the mantle with the Kodak grey scale Color Separation Guide (see Olsen, 2018). This scale contains 20 equal divisions, from 0 (pure white) to 19 (total black), made for adjusting grey tones in analogical photography. Kodak 3–5 is pale grey, 6–8 medium grey, 9–11 pale slaty-grey, 12–14 dark slaty grey and 15–17 slaty black. For each taxon, we collected the range of grey values from Howell and Dunn (2007) and Olsen (2018) and retained the mean value (called KGS hereafter; Figure 2b). When some subspecies did not exhibit variation in mantle colouration according to the literature, we kept the value of the nominal subspecies. We did not find published KGS values for *Larus novaehollandiae* and its two subspecies. For these taxa, we estimated the KGS values from HBW illustrations (del Hoyo et al., 2019). To do so, we first measured the modal luminance level in HBW illustrations, for the mantle of 20 taxa with known KGS value, using IMAGEJ software (Schneider, Rasband, & Eliceiri, 2012; using the mean luminance level yielded similar results). We then optimized a linear regression model between the known mean KGS values and the modal luminance levels ($R^2 = .87$), and used this model to predict KGS from the luminance level measured on illustrations of missing taxa (see details in Supporting Information Appendix S3).

The proportion of black on wingtips (PB hereafter) was measured from digital pictures of adult birds. For each taxon, we analysed between 2 and 5 photographs (mean = 4.6) of different individuals retrieved from the internet (all identifications were validated by ourselves; see the Table S1 in Supplementary Material with links to all retrieved photographs) and from our own picture collections. Photographs were selected to show birds in flight with one wing held flat and perpendicular to the camera (see Figure 1). Moreover, we included only pictures of birds without missing or moulting feathers. We used the GIMP software (gimp 2.10.12, The GIMP Development Team, 2019) to calculate the area (in pixels) of the outer wing (i.e., the hand, including the 10 primary feathers, greater and lesser primary coverts and the alula), and then the area of black pixels within the outer wing after thresholding the image to 25% luminance. PB was eventually calculated as the average, over all photographs of a given taxon, of the ratios of these two areas (i.e., black area/wing area); PB thus varies between 0 and 1 (Figure 2b). The only two taxa with grey wingtips were omitted from the analysis. Indeed, the grey colour is also produced by melanins and it is thus possible that the

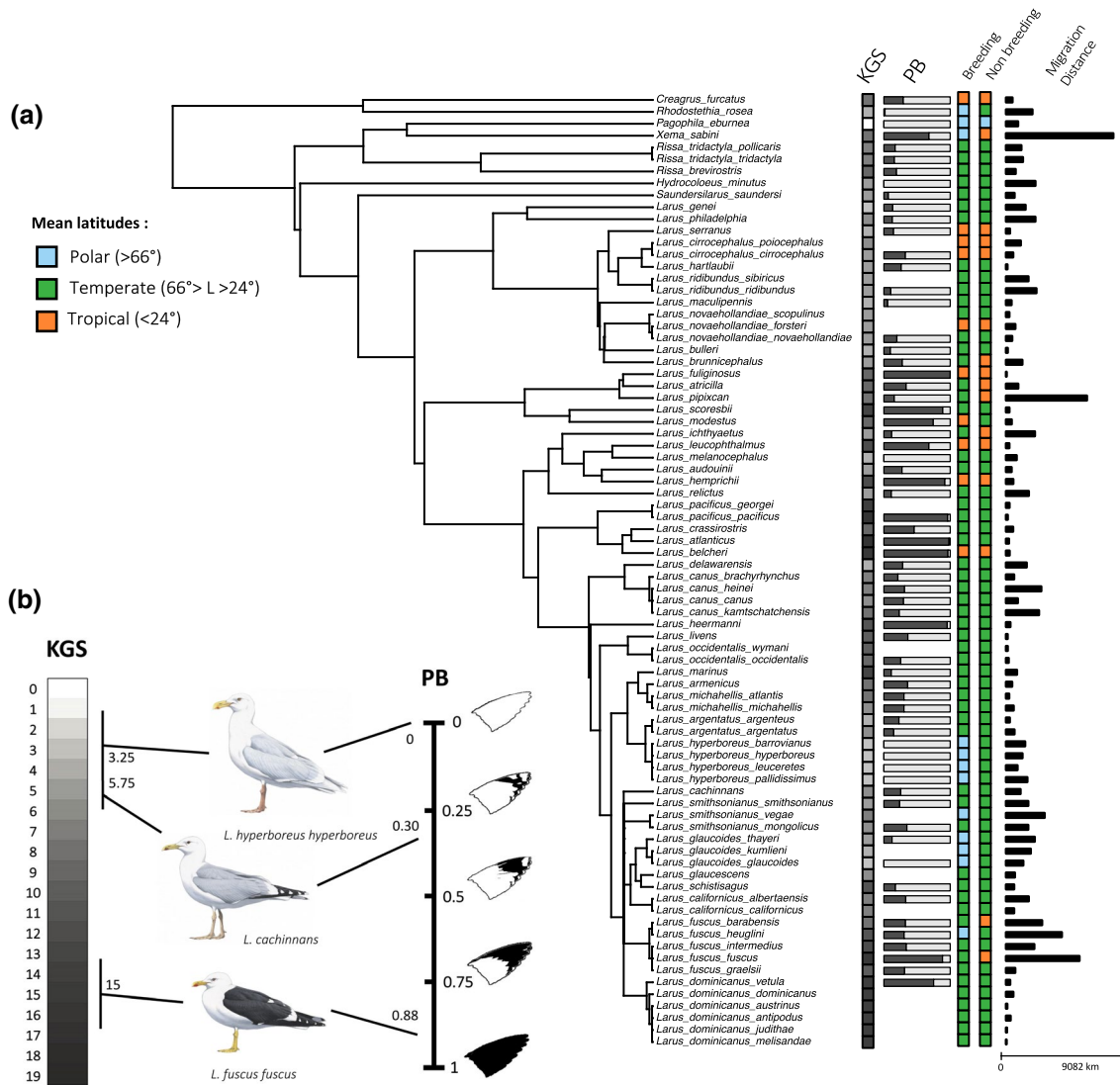


FIGURE 2 (a) The maximum clade credibility tree of gull taxa and their plumage colour (KGS = mantle colour; PB = proportion of black on wingtips). Rectangles with relative black proportion represent the PB value for each taxon; no rectangle means that the species was omitted for data availability reasons. The mean latitude of breeding and non-breeding regions is represented by a three-class (polar, temperate, tropical) variable. The migration distances between breeding and non-breeding regions are indicated with horizontal bars. (b) Examples of KGS and PB values for three taxa. Illustrations © HBW Alive/Lynx Edicions [Colour figure can be viewed at wileyonlinelibrary.com]

keratin feathers of these two taxa (*Larus glaucescens* and *Larus glaucooides kumlieni*) are more effective at resisting abrasive wear than white keratin feathers (see Bonser, 1995; but also Voitkevitch, 1966). Because of this uncertainty we preferred not to consider them rather than considering they had an entirely white wing tip. Finally, as we could not find appropriate photographs for several of the subspecies, PB was calculated for 65 taxa (82%) out of the 80 species and subspecies (see Figure 2b).

2.3 | Environmental data

Many gull species spend part of their non-reproductive season at sea. For this reason, we analysed climatic variables available for both land and water surfaces. In relation to the possible photo-protective

and UV-resistance function of gull plumage, we extracted an insolation variable defining the solar irradiance energy received on the Earth's surface in W/m^2 (Clouds and the Earth's Radiant Energy system, Nasa Earth Observations; <https://neo.sci.gsfc.nasa.gov/>). Monthly averaged measurements were downloaded for the entire period of available data (from 2006 to 2018). As we hypothesized a thermoregulation function of mantle colouration, we also considered a temperature variable by combining air and sea temperatures into a single variable describing the ocean and terrestrial monthly average temperature. Monthly averages of mean air temperature (from 1960 to 1990) were extracted from the WorldClim database (Hijmans et al., 2005) and monthly averages of mean sea surface temperature (from 1971 to 2000) were provided by the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Division (<http://www.esrl.noaa.gov/psd>). We checked the correlation

TABLE 1 Average values of generalized least square phylogenetic models applied to all topologies of phylogenetic trees. For each plumage variable [a: colour of the mantle (KGS); b: proportion of black on wingtips (PB)], models were performed with climatic conditions encountered either during the breeding or non-breeding period. Lambda values (Pagel, 1999) indicate the phylogenetic correlation parameter.

	Model	AIC	Variable	Estimate	SE	t-value	p-value	Lambda
(a)	KGS	383.2	Intercept	6.90	4.83	1.43	.157	.98
			<i>Breeding</i>	Insolation	-3.08	1.23	-2.50	
			Temperature	-1.83	1.50	-1.22	.225	
	<i>Non-breeding</i>		Insolation	9.54	1.56	6.11	< .001	
			Temperature	-5.61	1.64	-3.42	< .001	
(b)	PB	-9.93	Intercept	0.07	0.19	0.37	.710	.85
				Migration	0.05	0.52	0.10	
	<i>Non-breeding</i>		Insolation	0.47	0.17	2.72	.009	
			Migr. × Insol.	1.05	0.58	1.83	.072	
	<i>Breeding</i>		Insolation	0.37	0.16	2.32	.024	
			Migr. × Insol.	-4.39	1.08	-4.05	< .001	

AIC = Akaike's information criterion.

between air temperature and sea surface temperature in grid cells of coastal areas, where both variables were available (see Supporting Information Appendix S1, Figure S1). These climatic variables were also gridded at 10-min resolution to match distribution data.

We considered December, January and February as the winter period and June, July and August as the summer period, and assumed that these are the main breeding and non-breeding seasons for the focal species in the Northern Hemisphere (reversed for species breeding in the Southern Hemisphere). The remaining months were considered migration periods; environmental data for these months were not used in our analyses. Environmental variables were calculated for both boreal and austral locations, and for winter and summer periods. We made the assumption to assign northern summer to all breeding ranges above the equator (and vice versa for the Southern Hemisphere). Overall, we analysed five environmental variables: mean insolation during breeding (INSOL breeding) and non-breeding (INSOL non-breeding) periods, mean temperature during breeding (TMEAN breeding) and non-breeding (TMEAN non-breeding) periods, and mean migration distance (DIST migration).

In order to test all possible climatic effects of Gloger's rule as defined by Rensch (1929) (i.e., precipitation and temperature), we conducted a separate analysis to test the influence on KGS and PB of precipitation conditions encountered during either the breeding or non-breeding period on all species. Because these data are available only for the terrestrial and coastal regions (Karger et al., 2017; <http://chelsa-climate.org/>), not for marine regions, we considered only the terrestrial and coastal occurrence of the species.

2.4 | Statistical analysis

With the R package *phylolm* (Tung Ho & Ane, 2014) we fitted phylogenetic generalized least squares (PGLS) models to test how our

environmental explanatory variables correlate with the two colour variables (KGS and PB), while controlling for phylogenetic relatedness with the Pagel's lambda (Pagel, 1999). All variables were centred and scaled prior to analyses to facilitate interpretation (effect sizes were obtained from regression coefficients of the model; Schielzeth, 2010) and correlations between climate variables were examined to highlight potential collinearity effects (Supporting Information Appendix S1, Figure S2). We tested the importance of interaction effects between variables and removed them when not significant. All analyses were carried out on the MCC tree and on the 470 tree topologies in order to account for phylogenetic uncertainty.

To understand whether the geographical distribution of colouration in gulls is influenced by the seasonality of environmental conditions, for each colour metric we performed models that considered climatic conditions encountered during the breeding period and the non-breeding period for each colour index. For models with mantle colouration (KGS) as the response variable, we included temperature and insolation of breeding and non-breeding periods as explanatory variables: we expected that a thermoregulatory function of KGS would lead to a negative correlation between KGS and temperature while a photoprotective function of KGS would generate a positive correlation between KGS and insolation. For models with the amount of black on wingtips (BP) as the response variable, we included the migration distance and the insolation in both periods as explanatory variables. This allowed us to test the hypothesis that the proportion of black on wingtips increases feather resistance in taxa experiencing high solar radiation in winter regions and/or travelling over long distances.

Finally, in order to test the importance of considering intraspecific variation of subspecies, we replicated all analyses at the species level (52 species) by averaging subspecies values for the plumage and climatic variables. We conducted these analyses on the MCC tree pruned to match the species list using the *ape* package (Paradis & Schliep, 2018).

3 | RESULTS

The mantle colour of gulls (KGS) ranged from 0 (white, *Pagophila eburnea*) to 19 (black, *Larus atlanticus*, *Larus pacificus pacificus*) with a mean of 7.35 and standard deviation (SD) of 3.54. The proportion of black on wingtips (PB) ranged from 0 (8 taxa, see Supporting Information Figure S3) to 1 (*Larus fuliginosus*) with a mean of .32 and SD of .29. The within-taxon SD of PB ranged from 0 to .25 with a mean of .03 (for KGS the literature we used only reported range and not variance so we cannot compute a within-taxon SD for KGS).

We found that variations of mantle colour and wingtip pattern across taxa responded to climatic conditions of both breeding and non-breeding seasons but that conditions experienced during the non-breeding season had a stronger effect than the conditions of the breeding season (Table 1). For mantle colour (KGS), climatic variables of the non-breeding period had lower *p*-values and bigger effect sizes than for the breeding period (Table 1). For black proportion on wingtips (PB), the differences between breeding and non-breeding climatic conditions were weaker, but again with a lower *p*-value consistently observed for climatic variables encountered during the non-breeding period (alone or in interaction with migration distance; Table 1).

Comparative models indicate a strong phylogenetic signal for both KGS and PB (Table 1), indicating that at the scale of our analysis gull colouration is strongly determined by shared ancestry. Nevertheless, we found consistent results between the different tree topologies investigated (Supporting Information Table S2), which suggests that phylogenetic uncertainty does not impact our results. Last, replicating our analyses at the species level yielded qualitatively similar results (see Table S1 in Supporting Information Appendix S1), yet with lower phylogenetic signal. This result indicates that the high phylogenetic signal most likely results from closely related subspecies having similar plumage characteristics.

We found a positive effect of insolation during the non-breeding period on KGS, meaning that darker-mantle taxa (KGS > 10) predominantly winter in more highly insolated areas compared to

lighter-mantle taxa (KGS 4–7, Figures 3 and 4a). By contrast, we found a negative effect of non-breeding range temperature on mantle colour, with darker-mantle taxa wintering in colder areas than lighter-mantle taxa (those varying between KGS 4–7), even when controlling for insolation.

The interaction between insolation and migration distance was the most influential factor explaining interspecific variation in PB (Table 1), yet with opposite effects between breeding and non-breeding seasons. A positive effect for non-breeding conditions indicates that the higher the insolation, the greater the effect of migration distance on PB (Figure 4b). This suggests that PB increases for taxa that travel long distances and experience more highly insolated conditions during the non-breeding period. For climatic conditions of the breeding season, the opposite effect suggests that non (or moderate) migratory taxa that occupy areas with low insolation have less black on wingtips (Figure 4b). We also found that insolation conditions during the non-breeding season are positively correlated with PB but we found no effect of migration distance and insolation conditions during the breeding season alone.

We found no influence of precipitation conditions on mantle colouration (Supporting Information Table S3). However, we found that precipitation conditions encountered outside the breeding season, and in particular the interaction between these conditions and the migration distance, had a positive influence on the distribution of the proportion of black on wingtips (PB; Supporting Information Table S3). This suggests that PB increases for taxa that travel long distances and experience more rainy conditions during the non-breeding period.

4 | DISCUSSION

The study of animal colouration has played a major role in understanding the basic process of natural selection (Kettlewell, 1961) and how multiple and variable selective forces interact to shape

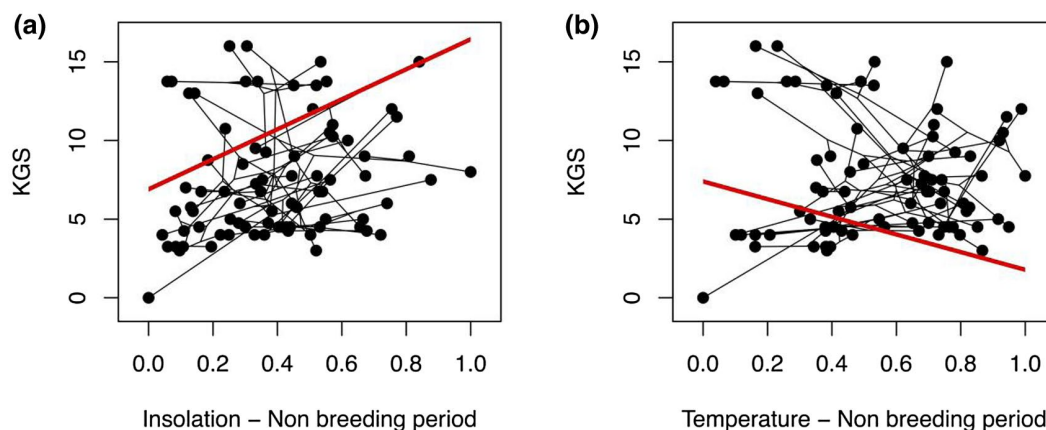


FIGURE 3 Relationship between mantle colour (KGS) and climatic variables (a: insolation; b: temperature) estimated from non-breeding ranges. Thin black lines represent the phylogenetic relatedness between taxa. Thick red lines represent the regression line of phylogenetic generalized least squares (PGLS) models (drawn with the R package *phytools*; Revell, 2012) [Colour figure can be viewed at wileyonlinelibrary.com]

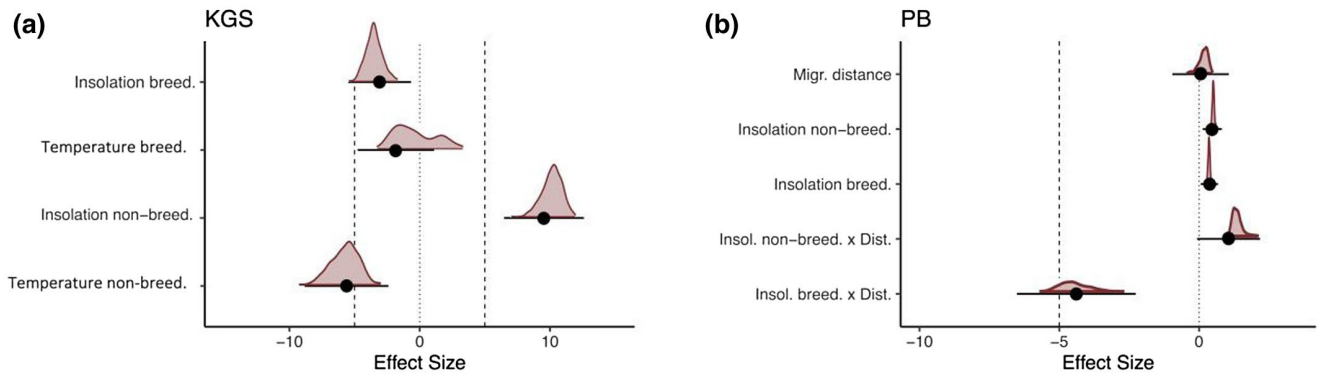


FIGURE 4 Forest plot of effect sizes and their 95% confidence intervals for mantle colour (a: KGS) and black proportion on wingtips (b: BP). Black dots and segments indicate effect sizes and confidence intervals for correlations with climatic variables accounting for the maximum clade credibility (MCC) tree. Red density curves show the distribution of effect sizes over 500 alternative tree topologies [Colour figure can be viewed at wileyonlinelibrary.com]

phenotypes (Cuthill et al., 2017). Recently, an extensive research agenda has highlighted the influence of climatic conditions on animal colouration. However, because climatic conditions are determined by several environmental variables (e.g., humidity, temperature, solar radiation) that can interact and vary throughout the life cycle of an animal, the precise role of climate in explaining the evolution and geographical distribution of animal colouration remains unclear. Here, we investigated the effect of seasonality in climatic conditions experienced by populations on the geographical distribution of plumage colouration in gulls. We found that colouration in gulls is more influenced by the environmental conditions encountered during the non-breeding period more than by conditions experienced during the breeding period. This result highlights that accounting for seasonality, whether it is due to moving between different environments or to remaining in a single seasonal environment, is crucial for understanding the biogeographical rules of animal colouration.

4.1 | Darker mantle provides feather protection and thermoregulation

We found that darker mantle colouration is positively correlated with insolation, and negatively with air temperature. The fact that lighter birds tend to inhabit the warmer areas matches the predictions of Bogert's rule (Clusella-Trullas et al., 2007). In contrast, we did not find support for Gloger's rule since we revealed that mantle colour does not seem to be influenced by precipitation conditions. Thus, gulls seem to differ from passerines (Delhey et al., 2019), in which lighter birds also inhabit warm areas (thus following Bogert's rule), but darker species tend to inhabit more humid habitats (thus following Gloger's rule).

Our results also suggest that the grey shade of the mantle plays a role in both thermoregulation and protection against solar radiation. In support of the thermoregulatory function, several dark-mantled taxa occupy high latitudes (polar and north-temperate regions) all year round where temperatures are cold especially outside the breeding period. Although heat transfer through bird plumage is complex,

Walsberg and Wolf (2000) suggested that darker coats (hence those with greater absorptivity) acquire greater heat loads from solar radiation than do lighter plumages. This assumption is mostly based on a study by Lustick et al. (1978), who found that skin temperatures is higher under dark plumage than under white plumage in *Larus argentatus*, which suggests that dark plumage has a higher radiative heat load. In the same study, the authors also showed that gulls orient themselves towards the sun when the solar irradiation becomes too intense, such that only the white surfaces of their bodies are exposed to the sun in order to decrease the absorption of solar radiation. These two results strongly suggest that a large surface of dark plumage facilitates body warming in very cold climates, where day length is generally reduced (see also Clusella Trullas et al., 2007). In support of the photoprotective function of mantle colouration, several dark-mantled taxa occupy strongly insolated environments, especially during the winter period. For example, within the *Larus fuscus* complex the darkest subspecies winter in the most insolated areas even though all subspecies nest at roughly similar latitudes (see Bergmann, 1982). Dark plumages presumably confer protection against solar radiation because melanin pigments increase the resistance of feathers against UV abrasion (Bergman, 1982; Bonser, 1995). Yet several species seem to deviate from the general pattern we described among gull taxa: for example, the all-white *Pagophila eburnea* and taxa of the *Larus glaucooides* and *Larus hyperboreus* complexes experience cold temperature during the non-breeding period while displaying very light body colouration (see Olsen, 2018). For these species occupying open polar regions, it has been proposed that white feathers would confer a thermal advantage by acting like optical fibres conducting solar energy to the skin (Grojean, Sousa, & Henry, 1980; Reynolds & Lavigne, 1981; but see Zimova et al., 2018).

4.2 | Black on wingtips may provide feather resistance to wear

The proportion of black on wingtips was mostly influenced by the positive interaction between insolation and migration distance, and

by the interaction between the amount of precipitation encountered during the non-breeding season and migration distance. The influence of precipitation should be interpreted with caution, though, because only a fraction of the geographical distribution of species was included in this analysis. Our results however bring much more support to the prediction that birds travelling long distances and overwintering in highly insolated areas have more black on wingtips. In contrast, sedentary species inhabiting areas of low insolation have less black on wingtips. This result is explained by the observation that melanin pigments reduce damage to keratin induced both by UV (Bergmann 1982; Borgudd, 2003) and abrading particles (Bonser, 1995). Species with a high proportion of black are thus more likely to tolerate long migration distances, which may cause mechanical damage, and more likely to spend the winter in highly insolated conditions where UV radiation can also damage their plumage. In addition to their role in photoprotection, thermoregulation, and resistance to abrasion by particles, melanin pigments may also increase the resistance of feathers to bacteria (e.g., Burt & Ichida, 2004; Goldstein et al., 2004), particularly in humid environments where bacteria can have higher keratinolytic capacities than those from arid regions (Burt & Ichida, 2004). It is thus possible that the melanin in the mantle and wingtips also plays this function in gulls, although this prediction requires further analyses.

4.3 | Perspectives on the study of gull colouration

In this study, we have only considered adult plumages because they vary little within taxa and are relatively easy to describe. However, as explained in the Introduction, they are shaped by the interplay of natural and sexual selection. Immature plumages (at least in the first age-classes) are very different from adult plumages and are presumably not influenced by sexual selection, so they could provide an even more direct test of the effects of climate on plumage evolution. Unfortunately, the immature plumages of gulls show complex variations, as all species go through several successive plumages between their juvenile (sporting usually for a very short time) and full adult plumage. Adult plumage is obtained between 2 full years (e.g., *Larus ridibundus*) and 4 years (all large white-headed gulls), making interspecific comparisons even more complicated to design. In addition, the first age-classes (especially juvenile and first-winter plumage) of large white-headed gulls are tricky to characterize as plumage patterns are complex (many feathers have an intricate pattern of dark and pale elements). Furthermore, even within a given age-class immature plumages can change rapidly due to variable timing and extent of moult and to feather wear; as a result the amount of inter-individual variation within taxa is often perplexing. Last, the distribution and migration patterns of immature birds can differ from those of adult birds (e.g., Marques et al., 2009). For all these reasons, investigating the links between abiotic environmental conditions and immature colouration would require a dedicated study, probably requiring more sophisticated methods to quantify plumage darkness.

Since the main aim of our study was to test whether breeding or non-breeding climate contributes most to plumage evolution, we did not include head colouration, which is seasonally variable in most species: dark hoods sported in breeding plumage usually disappear in winter while many species that are white-headed in breeding plumage develop dark streaks in winter. Furthermore, dark hoods are presumably under intense sexual selection as they are lost outside the breeding season and the size influences mate choice (Indykiewicz et al., 2017; Minias & Janiszewski, 2020). In addition, studying head colouration would require a more sophisticated measurement of melanism in order to accommodate the variable patterns of head colouration, from the grey to brown head streaking developed by many large white-headed gulls in winter to the uniform dark hood exhibited by other species in breeding plumage. Indeed, hood presence/absence in breeding plumage only loosely captures the quantitative variation of head colouration among hooded species, which ranges from light grey in *Larus cirrocephalus* to jet black in, for example, *Larus leucophthalmus* (Olsen, 2018). In spite of these limitations, Minias and Janiszewski (2020) found that hood occurrence in gulls was less frequent at higher latitudes. This result is at odds with our findings that melanism tends to decrease at higher latitudes (lighter mantle colour at higher latitude). However, the effect of latitude on melanism in our study was mainly apparent when considering non-breeding climate, whereas hood occurrence is limited to the breeding season. Taken together, these findings reinforce our hypothesis that hood occurrence may be subject to other selection pressures than the colouration of the rest of the plumage. A study of head plumage evolution incorporating age- and season-related variations should thus allow us to better understand the interplay between sexual and natural selection in gull plumage evolution.

4.4 | Conclusion: how ubiquitous is the influence of seasonality on the evolution of avian colouration?

Gulls have several biological traits that are not ubiquitous in birds. Firstly, many species of gulls are migratory but a large majority of bird species are sedentary (Eyres, Böhning-Gaese, & Fritz, 2017). Indeed, several previous studies on avian colouration focused on clades made up mostly of non-migratory species (for example Australian birds that mostly undertake nomadic movements in Dalrymple et al., 2018; Delhey, 2018; Friedman & Remeš, 2017). In addition, gulls exhibit limited seasonal change in colouration while many other birds undergo marked seasonal changes (see Dale, Dey, Delhey, Kempnaers, & Valcu, 2015; McQueen et al., 2019). Finally, gulls occupy open environments and the selective pressures on their plumage are potentially different from those of birds that occupy other environments. For example, we would expect a limited effect of vegetation cover on the colouration of adult gulls whereas vegetation has a major effect on colouration in passerine birds (Delhey et al., 2019). Likewise, it has also been shown in Procellariiformes that the distribution of colouration appears to be related to feeding

ecology and species behaviour at sea (Bretagnolle, 1993) with solitary feeding and 'squid eaters' being large white species, whereas flock-feeding or diving 'fish eaters' tend to have cryptic and darker plumage to escape predation or to benefit from counter shading as an adaptation to fish behaviour.

However, our finding that colouration in gulls is influenced by the climatic conditions experienced during the non-breeding season is likely to extend to many other bird species, even though selection pressures may vary among taxonomic groups (e.g., Friedman & Remeš, 2017). A large proportion of birds perform seasonal movements (see the different types of movements in Eyres et al., 2017; Rappole, 2013) and many migratory birds spend more time on migration and in the non-breeding grounds than on the breeding grounds (see e.g., Jacobsen et al., 2017). For those species that migrate and that do not change plumage between the breeding and non-breeding season, colouration should be influenced by non-breeding as much as, or even more than, breeding climatic conditions. Our results thus highlight the importance of taking into account seasonality and migratory movements to understand global spatial patterns of animal colouration and suggest that the effects of seasonality we uncovered in gulls could also apply to many other animals that perform seasonal movements or experience seasonal changes in their climatic niches.

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DATA AVAILABILITY STATEMENT

Some data are publicly available; bird range maps at www.birdlife.org, environmental data at www.worldclim.org, <http://www.esrl.noaa.gov/psd> and <https://neo.sci.gsfc.nasa.gov/>, and bird phylogenetic data at www.birdtree.org. A table (Table S2) reporting plumage colouration and migration data for each species and subspecies is available in the Supporting Information, as well as a table (Table S1) containing the internet links to access all the photos used in this study.

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BIOSKETCH

Paul Dufour is an experienced field ornithologist with a broad interest in the ecology of birds who currently focuses on the evolution of long-distance avian migration for his PhD. He worked on this project with a MSc student, Julia Guerra Carande, who is interested in the biology of animal colouration. The other co-authors are all interested in evolution and ecology with focuses on the evolution of phenotypes and signals (JPR and PAC) or macroevolution and global biodiversity patterns (SL and JR).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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