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Clear correlations between human and bird visual assessments of color have been documented, and are often assumed, despite fundamental differences in human and avian visual physiology and morphology. Analyses of plumage colors with avian perceptual models have shown widespread hidden inter-sexual and inter-specific color variation among passerines perceived as monochromatic to humans, highlighting the uncertainty of human vision to predict potentially relevant variation in color. Herein, we use reflectance data from 13 *Larus* gull species as an exemplar data set to study concordance between human vision and avian visual modeling of feather colors near, or below, the human threshold for discrimination. We found little evidence among gulls for sexual dichromatism hidden from human vision, but did find inter-specific color variation among gulls that is not seen by humans. Neither of these results were predictable *a priori*, and we reassert that reflectance measurements of actual feather colors, analyzed with avian relevant visual models, represent best practice when studying bird coloration.

Introduction

Since Darwin (1871) and Wallace (1889) animal coloration has been a focus for biologists, and in particular the importance of studies on coloration in birds for understanding behavior and evolution cannot be overstated (e.g., Hill & McGraw 2006a, 2006b). Humans and most avian species are visually oriented, diurnal animals, so we often assume that our visual perceptions of color are the same. However, fundamental differences in color vision between birds and humans exist because birds possess four spectrally distinct single-cone cell photoreceptors (humans possess only three; *see* Jacobs 2018), each associated with a pigmented oil droplet, and one sensitive to ultraviolet (UV) wavelengths (Cuthill *et al*. 2000, Hart 2001, Hart & Hunt 2007). Birds also possess double-cone cells, which are suggested to play a role in achromatic vision (perception of form and motion), possibly through detection of luminance variation (Osorio & Vorobyev 2005, Hart & Hunt 2007, Lind *et al*. 2014). Avian perceptual color space can then be modeled as a tetrahedral volume (e.g., Endler & Mielke 2005, Stoddard & Prum 2008), and discrimination of colors within the volume can be predicted given the assumption that visual performance is receptor-noise limited (Vorobyev & Osorio 1998, Vorobyev *et al*. 1998). Predictions from receptor-noise limited models fit well with behavioral data for discrimination of color across a broad range of taxa (Kelber *et al*. 2003, Kelber & Osorio 2010, Lind *et al*. 2014, Olsson *et al*. 2015).

Given the physiological differences between bird and human vision, modeling based on avian photoreceptor physiology likely represents the most appropriate method to quantify bird coloration. Such modeling of reflectance data collected from feathers has shown widespread examples of variation in avian coloration potentially visually discernible to birds (e.g., sexual dichromatism, and inter-specific color divergence) but not to humans (e.g., Mennill *et al*. 2003, Mays *et al*. 2004, Eaton 2005, 2007, Armenta *et al*. 2008, Benites *et al*. 2010, Seddon *et al*. 2010, Burns & Shultz 2012, Wilson *et al*. 2012, Hernández-Palma 2016). And yet, there are studies documenting correlations between human and bird assessments of coloration (Armenta *et al*. 2008, Seddon *et al*. 2010, Bergeron & Fuller 2018). So, when can human vision accurately predict color variation relevant to bird vision? We assert that discrimination of plumage colors by birds that appear very similar or identical to human vision (i.e., assessing sexually monochromatic *vs*. sexually dichromatic plumages, or inter-specific color divergence) remains unpredictable *a priori*, and this necessitates collecting reflectance data from feathers and using avian visual models to quantify all relevant color variation.

The primary aim of our study was to use plumages of 'white-headed' gull species (genus *Larus*) as a model data set to examine gull feather colors that are near, or below, the human visual threshold for color discrimination. Gull plumage colors generally appear white, grey and black, presumably due to both melanin pigmentation and structural coloration (Hill & McGraw 2006a). To our knowledge, species within this genus have only been described based on human vision as exhibiting sexually monochromatic plumages (e.g., del Hoyo *et al*. 1996, Arizaga *et al*. 2008), indicating that to date humans have not visually identified sex-specific color differences among gulls (i.e., no sexual dimorphism in plumage color or pattern). Furthermore, inter-specific variation in gull plumage coloration can also appear ambiguous to human vision, making species identification difficult in field settings (del Hoyo *et al*. 1996). Given the fundamental differences in color vision between humans and birds, namely trichromacy *vs*. tetrachromacy (Jacobs 2018), and that these visual differences result in different human and bird interpretations of the same plumage colors (e.g., Vorobyev *et al*. 1998, Kelber *et al*. 2003, Håstad & Ödeen 2008), we sought to test these previous human 'assumptions' of gull plumage coloration. Hence, we used spectral reflectance data of feather colors from 13 *Larus* species, combined with avian visual models (Vorobyev & Osorio 1998, Stoddard & Prum 2008), to quantify gull plumage colors and address two main questions: (1) do gull plumages exhibit sexual dichromatism from an avian visual perspective?, and (2) do gull plumages exhibit inter-specific plumage coloration from an avian visual perspective?

Methods

Spectral analysis of plumage colors

Spectral reflectance data were collected from museum specimens at the Smithsonian Institution National Museum of Natural History of male and female gulls (genus *Larus*) in adult plumages across 13 species (Table 1, for sample sizes *see* Table 2). Measurements were taken from six

Table 1. Avian perceptual color space distances (ΔS, in jnd) for all homologous male/female plumage patch comparisons among 13 'white-headed' *Larus* gull species, with associated 95% confidence intervals (CI) and PERMANOVA *F* statistics (*see* Methods; for sample sizes for each sex *see* Table 2). Values in boldface indicate plumage patches above 1.0 jnd threshold for discrimination as different colors, and/or having significant difference in male and female color (* = $p < 0.05$, ** = $p < 0.01$).

Species	Plumage patch					
	forehead	back	wing coverts	throat	chest	primary
Larus heermanni						
ΔS	0.467	**1.081**	0.174	**1.279**	0.649	0.624
95%CI	0.164–1.589	0.261–2.041	0.086–1.019	0.396–2.578	0.258–1.026	0.237–1.606
$F_{1,6}$	0.292	1.955	0.265	1.741	3.757	0.790
L. delawarensis						
ΔS	0.585	0.414	0.146	0.816	0.387	0.554
95%CI	0.08–1.855	0.08–1.707	0.05–1.042	0.096–1.778	0.141–1.629	0.222–1.614
$F_{1,12}$	0.755	0.394	0.143	1.664	0.305	0.475
L. canus						
ΔS	**2.331**	0.644	0.987	**1.985**	**1.626**	0.323
95%CI	1.083–3.647	0.132–1.394	0.273–1.661	0.487–3.508	0.811–2.589	0.079–1.28
$F_{1,12}$	**6.105***	3.040	**4.372***	3.089	**4.888****	1.365
L. californicus						
ΔS	**1.108**	0.735	0.406	0.828	0.515	0.449
95%CI	0.16–2.441	0.149–1.332	0.06–0.913	0.084–2.189	0.094–1.412	0.116–0.905
$F_{1,8}$	1.188	2.669	0.836	0.824	**2.782***	1.947
L. argentatus smithsonianus						
ΔS	**1.766**	**1.282**	**1.060**	**1.731**	**1.200**	**1.538**
95%CI	0.211–3.572	0.488–2.485	0.173–2.277	0.305–3.094	0.437–1.92	0.853–2.203
$F_{1,13}$	2.770	**3.843****	2.139	2.789	**4.527***	**7.629***
L. thayerii						
ΔS	0.581	0.438	0.451	0.522	0.278	0.734
95%CI	0.076–1.162	0.041–1.332	0.056–1.242	0.082–1.041	0.107–0.767	0.107–1.952
$F_{1,12}$	**4.006***	0.925	0.791	1.477	0.737	2.496
L. fuscus						
ΔS	0.624	0.950	**1.149**	0.658	0.377	0.651
95%CI	0.102–1.648	0.18–1.973	0.219–2.317	0.088–1.51	0.071–1.171	0.174–1.819
$F_{1,10}$	1.525	1.930	2.199	1.740	2.253	0.669
L. dominicanus						
ΔS	0.286	0.731	0.706	0.433	0.747	0.088
95%CI	0.062–1.237	0.245–1.228	0.151–1.273	0.062–1.16	0.112–1.407	0.095–0.953
$F_{1,14}$	0.292	**4.918***	**5.271***	0.855	2.642	0.022
L. glaucescens						
ΔS	0.697	0.163	0.516	0.476	0.172	0.213
95%CI	0.107–2.048	0.081–0.765	0.084–1.153	0.106–1.955	0.053–0.764	0.098–1.233
$F_{1,14}$	0.728	0.523	**4.483***	0.222	0.620	0.269
L. hyperboreus						
ΔS	0.341	0.201	0.646	0.370	0.627	0.360
95%CI	0.059–1.447	0.042–0.825	0.083–1.369	0.052–1.344	0.166–1.245	0.07–1.235
$F_{1,17}$	0.604	0.926	2.134	0.351	1.582	0.202
L. michahelles						
ΔS	0.767	0.664	0.496	**1.025**	0.664	0.444
95%CI	0.445–1.099	0.581–0.753	0.398–0.603	0.712–1.35	0.602–0.737	0.345–0.587
$F_{1,1}$	1.177	12.944	4.664	2.239	12.935	1.606
L. occidentalis						
ΔS	0.250	0.474	0.299	0.490	0.737	0.699
95%CI	0.065–1.114	0.132–0.923	0.071–0.806	0.06–1.182	0.385–1.143	0.402–1.174
$F_{1,7}$	0.267	0.489	0.371	0.396	0.772	0.369
L. marinus						
ΔS	**2.156**	0.597	0.329	0.583	0.685	0.534
95%CI	0.991–3.377	0.267–1.155	0.091–0.723	0.275–2.084	0.251–1.19	0.274–0.896
$F_{1,3}$	4.678	1.328	0.940	0.158	1.863	1.243

Table 2. Average normalized brightness (Stoddard & Prum 2008) for all plumage patches for males and females, with associate two-tailed *t*-test statistics (*t* values with degrees of freedom, df, in parentheses). Values in boldface indicate feather patches significantly different between males and females within a species (* = $p < 0.05$, ** = $p < 0.01$).

Species	Plumage patch					
	forehead	back	wing coverts	throat	chest	primary
Larus heermanni						
male (*n* = 4)	0.544	0.103	0.090	0.446	0.255	0.050
female (*n* = 4)	0.610	0.098	0.090	0.443	0.226	0.043
t (df)	–1.581 (3.2)	0.941 (3.6)	0.113 (5.6)	0.104 (5.8)	1.684 (6)	1.811 (3.7)
L. delawarensis						
male (*n* = 7)	0.621	0.246	0.277	0.604	0.502	0.031
female (*n* = 7)	0.659	0.286	0.299	0.592	0.506	0.044
t (df)	–1.372 (11)	**–3.374 (10.9)****	–1.261 (10.2)	0.407 (10.7)	–0.174 (11.4)	**–3.095 (10.4)***
L. canus						
male (*n* = 6)	0.670	0.217	0.222	0.571	0.506	0.062
female (*n* = 8)	0.604	0.213	0.221	0.504	0.477	0.056
t (df)	**2.909 (11.8)***	0.436 (9.4)	0.1 (8.8)	1.917 (11.5)	1.686 (10.4)	0.789 (7.5)
L. californicus						
male (*n* = 5)	0.634	0.193	0.211	0.535	0.516	0.055
female (*n* = 5)	0.680	0.186	0.207	0.526	0.550	0.049
t (df)	**–2.495 (7.8)***	0.914 (7.6)	0.378 (4.7)	0.459 (8)	–1.47 (7.1)	1.35 (7.8)
L. argentatus smithsonianus						
male (*n* = 10)	0.598	0.277	0.284	0.497	0.532	0.057
female (*n* = 5)	0.596	0.264	0.276	0.525	0.524	0.061
t (df)	0.038 (6.8)	0.891 (7.7)	0.671 (10.9)	–0.942 (6.8)	0.438 (6.1)	–0.505 (6.1)
L. thayerii						
male (*n* = 7)	0.586	0.280	0.281	0.565	0.527	0.073
female (*n* = 8)	0.601	0.252	0.273	0.569	0.504	0.073
t (df)	–0.856 (12.8)	**2.646 (12.5)***	0.933 (12.4)	–0.307 (11.9)	1.146 (10.6)	–0.002 (13)
L. fuscus						
male (*n* = 6)	0.610	0.097	0.098	0.557	0.537	0.041
female (*n* = 6)	0.638	0.107	0.113	0.569	0.551	0.043
t (df)	–1.173 (6.8)	–0.971 (9.8)	–1.033 (9.5)	–0.528 (10)	–0.628 (9.9)	–0.8 (10)
L. dominicanus						
male (*n* = 8)	0.568	0.072	0.077	0.496	0.501	0.040
female (*n* = 8)	0.665	0.079	0.083	0.530	0.525	0.039
t (df)	**–4.673 (12.6)****	–0.934 (13.1)	–0.758 (13.8)	–1.222 (11.2)	–1.249 (13.4)	0.152 (11.9)
L. glaucescens						
male (*n* = 9)	0.640	0.239	0.251	0.531	0.519	0.194
female (*n* = 7)	0.675	0.245	0.245	0.575	0.530	0.181
t (df)	–1.551 (10.3)	–0.462 (11.2)	0.377 (10)	–1.37 (13.8)	–0.5 (13.8)	0.711 (9.3)
L. hyperboreus						
male (*n* = 9)	0.600	0.396	0.403	0.595	0.543	0.382
female (*n* = 10)	0.589	0.375	0.400	0.587	0.520	0.370
t (df)	0.566 (17)	1.694 (17)	0.221 (16.6)	0.503 (12.2)	1.422 (14.9)	0.879 (16.5)
L. michahelles						
male (*n* = 2)	0.744	0.275	0.257	0.551	0.558	0.048
female (*n* = 1)	0.655	0.26	0.276	0.525	0.563	0.052
t (df)	n/a	n/a	n/a	n/a	n/a	n/a
L. occidentalis						
male (*n* = 1)	0.547	0.135	0.121	0.483	0.513	0.043
female (*n* = 8)	0.615	0.13	0.135	0.478	0.496	0.043
t (df)	n/a	n/a	n/a	n/a	n/a	n/a
L. marinus						
male (*n* = 3)	0.601	0.082	0.083	0.553	0.501	0.039
female (*n* = 2)	0.601	0.089	0.085	0.522	0.51	0.041
t (df)	n/a	n/a	n/a	n/a	n/a	n/a

plumage patches for all individuals: forehead, back, wing coverts, throat, chest, primaries. We chose individual specimens in good plumage condition (i.e., no evident wear due to natural causes or storing conditions). Specimens sampled in the study ranged in collection age from > 100 years to < 5 years. While older specimens have been shown to potentially differ in feather reflectance properties, mainly brightness (e.g., Armenta *et al*. 2008, Doucet & Hill 2009), a preliminary analysis of the relationship between specimen age and normalized brightness of all feather patches, for each sex separately, showed no significant relationship between these variables for either sex (GLM male: $r^2 = 0.0325$, $p = 0.251$; GLM female: $r^2 = 0.00164$, $p = 0.404$). We therefore concluded that specimen age does not have a systematic bias impacting our overall results, and so specimen age was not incorporated in downstream analyses.

Plumage reflectance measurements were made with an Ocean Optics S-2000 spectrometer (Dunedin, Florida) equipped with a reflectance probe and a PX-2 pulsed xenon light source, calibrated against a Spectralon white standard prior to each measurement, at an angle of 90° relative to the feather surface. Reflectance data (percent light reflected at each wavelength) were collected from 300–700 nm with OOIbase32 software, then processed into 1 nm median value bins used in subsequent analyses.

Avian visual system modeling

We quantified gull coloration from reflectance data for each sex across all species on a patch by patch basis, and for whole plumages, using the *pavo* package (Maia *et al*. 2013). Within each species we calculated the average color difference between homologous male-female feather patches using the Vorobyev–Osorio (Vorobyev & Osorio 1998) receptor noise color discrimination model. The model returns a distance in perceptual color space, ΔS, in units of jnd (just noticeable differences), where 1.0 jnd is the threshold for discriminating two colors (Vorobyev *et al*. 1998, Vorobyev 2003). Given that calculations of ΔS values can be sensitive to the choice of visual model parameters, such as spectral sensitivity functions and/or photoreceptor densities (Bitton *et al*. 2017, Lind *et al*. 2017, Maia & White 2018), we used spectral sensitivity functions from the Eurasian blue tit (*Cyanistes caeruleus*) as a representative UVS-type visual system. This is largely justified given that gulls exhibit the UVS-type SWS1 photoreceptor and transparent ocular media (Håstad *et al*. 2009, Ödeen *et al*. 2010) like many passerines (Ödeen *et al*. 2011, Ödeen & Håstad 2013), and the overall similarity in sensitivity functions of SWS1 photoreceptors across a diversity of avian taxa (Hart & Hunt 2007). We used single-cone cell photoreceptor proportions (1:1.8:2.4:2.3) taken from a representative gull, *L. novaehollandiae* (Hart 2001). We chose daylight illuminant, D-65, and a 'ideal' background, as best representing the general ecological viewing conditions of most gulls. We considered intra-sexual variation to assess statistical significance of ΔS values, given they represent comparisons of average male and female colors (Maia & White 2018). For this, we determined if females and males are statistically separated in color space by calculating a distance based PERMANOVA on ΔS noise-corrected color distances using the *adonis* function of the *vegan* package (https://cran.r-project.org/web/packages/vegan/vegan.pdf). We then assessed whether the statistical separation is perceptually discriminable by estimating the geometric average of all ΔS values within each species and calculated the 95% confidence interval (CI) through a bootstrap analysis with the *bootcoldist* function of *pavo*. Taken together, a mean ΔS greater than 1.0 jnd (color discrimination threshold) with 95%CI above 1.0 jnd, and a PERMANOVA statistic significant at $p < 0.05$, indicates evidence for potential sexual dichromatism of a given homologous male-female feather patch comparison to avian vision (Eaton 2005, Maia & White 2018).

To compare gull coloration among species, we (i) calculated inter-specific ΔS on a patch-by-patch basis through the same bootstrap procedure as above (Maia & White 2018); (ii) calculated average color span (mean of all pairwise distances of points in tetrahedral color space; Stoddard & Prum 2008) and color volume (volume created by a convex hull around all modeled points in tetrahedral color space; Stoddard & Prum 2008) for both sexes within each

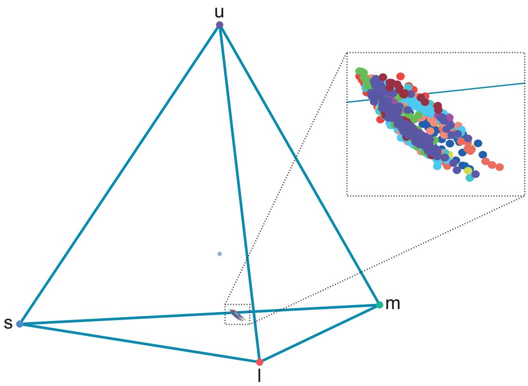

Fig. 1. Plot of reflectance data for all individual plumage patches measured from each species in avian tetrahedral color space. Vertices of the tetrahedron correspond to each of the four single-cone cells present in the avian retina (u = ultra-violet wavelength sensitive, s = short wavelength sensitive, m = medium wavelength sensitive, and l = long wavelength sensitive). Position of a given color in the tetrahedron is determined by the relative excitation of these four different cone cells. Magnification of all plotted gull plumage patches (each species color coded uniquely) on the right-hand side.

species; and (iii) calculated color volume overlap between each species for both male and female plumages.

We also calculated the normalized brightness, a potential achromatic visual signal perceived via the double cone-cells (Lind *et al.* 2014), for each plumage patch of each individual specimen (i.e., normalized brilliance in Stoddard & Prum 2008). We then calculated average normalized brightness for both sexes of each species, and performed two-tailed *t*-test to compare brightness within species between the sexes on a patch by patch basis. For three species (*L. marinus*, *L. michahelles*, *L. occidentalis*), *t*-test was not performed due to small sample sizes.

All coloration and statistical packages used in the analyses were implemented in R 3.5.1 (R Core Team 2018).

Results

A total of 78 comparisons were made between male and female feather patches across 13 species sampled (Table 1). Avian color discrimination models yielded ΔS values (in jnd) ranging from 0.088 (primary of *L. dominicanus*) to 2.331 (forehead of *L. canus*). Of these 78 inter-sexual comparisons, we found 15 feather patches (from 7 species) with $\Delta S > 1.0$ (19.2%), and two feather patches with $\Delta S > 2.0$ (2.6%). Of these 15 patches with ΔS values > 1.0, 9 were found on two species (6 feather patches on *L. argentatus smithsonianus*, and 3 feather patches on *L. canus*).

Among all 78 feather patch comparisons, we found 11 feather patches that were statistically different in color space between males and females (PERMANOVA: $p < 0.05$; Table 1), however, 6 of these patches were not above threshold for discrimination as different colors ($\Delta S < 1.0$), and another 4 were not reliably separated by sex in bootstrap analyses (i.e., 95%CI around mean ΔS contained 1.0 jnd; Table 1). We found only one statistically different feather patch, the forehead of *L. canus* (Table 1), with unambiguous evidence for sexual dichromatism (i.e., $\Delta S > 1.0$, 95%CI > 1.0, PERMANOVA: $F_{1,12} = 6.11$, $p = 0.013$).

We found 6 feather patches from 5 species that were statistically different in normalized brightness between males and females (Table 2). Only one of these patches, the forehead of *L. canus*, was also statistically different in coloration.

Calculations of whole plumage variables yielded average color span values that varied approximately two-fold, and color volumes ranged over two orders of magnitude across all species (Table 3). Gull plumages of these 13 species occupy similar tetrahedral color space (Fig. 1), and pairwise comparisons of species' color volumes show extensive overlap for both sexes (Appendix 1). Patch by patch comparisons across all 78 species pairs (e.g., comparing color between two males of different species), yielded 66 male species pairs (84.6%), and 54 female species pairs (69.2%), that had at least one plumage patch with $\Delta S > 1.0$ and 95%CI > 1.0, indicating evidence for visual discrimination of inter-specific plumage colors (Table 4, Appendixes 2 and 3).

Discussion

In general, gulls exhibit sexual dimorphism in size, with males usually larger, while they are only described as sexually monochromatic (e.g., del Hoyo *et al*. 1996, Arizaga *et al*. 2008). The white forehead of *L. canus* was the only feather patch we found with unambiguous evidence for avian visual discrimination of color between males and females (Table 1). We found statistical differences in brightness between males and females for 6 feather patches (Table 2), however interpreting thresholds for discrimination of differences in brightness, as an achromatic visual signal via the double-cone cells, remains uncertain (Osorio & Vorobyev 2005, Lind *et al* 2014, Günther *et al*. 2018), although brightness levels of plumages could play important evolutionary and ecological roles (e.g., Marcondes & Brumfield 2019). Hence, we interpreted our data to show little (1 of 13 species) evidence for sexual dichromatism from a gull visual perspective that is hidden to human vision. Our results contrast sharply with data from passerines, where numerous studies have documented widespread hidden color differences, including sexual dichromatism (e.g., Håstad *et al*. 2005, Eaton 2005, 2007, Armenta *et al*. 2008, Burns & Shultz 2012, Hernández-Palma 2016). This difference with our results cannot be simply attributable to differences in types of avian visual physiology, as gulls possess a UVS-type SWS1 photoreceptor (not the alternative VS type found among some birds; Ödeen & Håstad 2013), with UV-transparent ocular media (Håstad *et al*. 2009, Ödeen *et al*. 2010), similar to many passerine lineages (Hart & Hunt 2007, Ödeen & Håstad 2013).

Gull plumages encompassed a relatively narrow range of average color spans and color volumes (Stoddard & Prum 2011), they were very similar between the sexes, and they overlapped extensively between species (Fig. 1, Table 3 and Appendix 1). By comparison, New World bunting and Neotropical tanager species exhibit a variety of plumage colors and patterns resulting in limited plumage volume overlap between species, and average color spans at least double, and color volumes up to three orders of magnitude larger than that of gulls (Stoddard & Prum 2008, Shultz & Burns 2013). The relatively small variation in color spans and volumes among gull species sampled in this study likely reflects the limited diversity in plumage coloration (i.e., only blacks, whites, greys), and overall similarity in plumage pattern (del Hoyo *et al*. 1996). These data corroborate the sexually monochromatic aspects of gull coloration, and

Table 3. Male and female whole plumage variables for all species. Average color span denotes the average distance in a tetrahedral avian visual color space among the six plumage patches (forehead, back, wing coverts, throat, chest, primary) measured for all individuals of each sex for each species. Color volume represents the space occupied by a convex hull around these six plumage patches for all individuals as plotted in avian color space for each sex and each species (Stoddard & Prum 2008).

Species	Color volume	Average color span
Larus heermanni		
male	7.9×10^{-6}	3.3×10^{-2}
female	1.9×10^{-6}	3.3×10^{-2}
L. delawarensis		
male	3.0×10^{-6}	3.1×10^{-2}
female	2.8×10^{-6}	3.6×10^{-2}
L. canus		
male	1.4×10^{-6}	3.1×10^{-2}
female	4.3×10^{-6}	3.8×10^{-2}
L. californicus		
male	9.7×10^{-7}	3.3×10^{-2}
female	5.7×10^{-7}	3.4×10^{-2}
L. argentatus smithsonianus		
male	2.6×10^{-6}	3.3×10^{-2}
female	1.8×10^{-6}	3.6×10^{-2}
L. thayerii		
male	1.1×10^{-6}	3.6×10^{-2}
female	1.6×10^{-6}	3.7×10^{-2}
L. fuscus		
male	3.1×10^{-6}	3.8×10^{-2}
female	2.1×10^{-6}	3.8×10^{-2}
L. dominicanus		
male	2.4×10^{-6}	4.2×10^{-2}
female	2.1×10^{-6}	4.6×10^{-2}
L. glaucescens		
male	8.0×10^{-7}	2.8×10^{-2}
female	9.4×10^{-7}	3.0×10^{-2}
L. hyperboreus		
male	3.4×10^{-7}	2.0×10^{-2}
female	4.0×10^{-7}	2.2×10^{-2}
L. michahelles		
male	3.8×10^{-7}	3.4×10^{-2}
female	9.0×10^{-8}	3.5×10^{-2}
L. occidentalis		
male	1.9×10^{-7}	4.3×10^{-2}
female	4.3×10^{-6}	4.1×10^{-2}
L. marinus		
male	7.3×10^{-7}	3.7×10^{-2}
female	8.0×10^{-7}	4.5×10^{-2}

Table 4. Inter-specific visual comparisons of plumage color differences for both sexes (males lower diagonal, females upper diagonal) for all *Larus* species pairs. Plumage patches listed (location: fo = forehead, ba = back, wc = wing coverts, th = throat, ch = chest, pr = primary) for each comparison are those found to be above modeled threshold for avian visual discrimination (i.e., $\Delta S > 1.0$ jnd and 95%CI > 1.0 jnd; *see* Appendixes 2 and 3 for all values). Green font indicates species comparisons for which the forehead patch (fo) was modeled to be visually discernable to avian vision, while no known previous human visual assessments noted species-specific color differences for this plumage patch. Red font indicates species comparisons for which all six plumage patches measured were modeled to be visually indistinguishable, respective to one another, as different colors to avian vision (i.e., $\Delta S < 1.0$ jnd for each patch comparison; *see* Appendixes 2 and 3 for all values).

Larus species	*heermanni*	*delawarensis*	*canus*	*californicus*	*a. smithsonianus*	*thayerii*	*fuscus*	*dominicanus*	*glaucescens*	*hyperboreus*	*michahelles*	*occidentalis*	*marinus*
heermanni	–	fo, ba, wc, ch, pr	ba, wc, ch	all patches	ba, wc, ch	ba, wc, ch	fo, ba, wc, ch	ba, wc, ch, pr	fo, ba, wc, ch, pr	ba, wc, ch, pr	all patches	ba, wc, ch	ba, wc, pr
delawarensis	all patches	–	fo	none	pr	fo, th, ch, pr	none	fo, wc, ch	pr	th, pr	none	th	wc
canus	all patches	none	–	none	none	none	none	ba, wc	pr	pr	th	none	ba, wc
californicus	ba, wc, th, ch, pr	th, ch	ch	–	pr	fo, th, pr	none	none	pr	ba, pr	none	none	none
a. smithsonianus	all patches	none	none	none	–	none	ba	ba, wc	pr	pr	none	none	ba, wc, pr
thayerii	ba, wc, ch	fo, th, ch, pr	fo, th, ch, pr	pr	fo, th, pr	–	th	ba, wc	fo, th, pr	pr	fo, th	none	ba, wc, pr
fuscus	ba, th, ch, pr	fo, wc, th	wc	none	wc	ba, wc, pr	–	none	pr	ba, wc, pr	none	none	none
dominicanus	ba, wc, th, ch, pr	fo, ba, wc, th	ba, wc	ba, wc	ba, wc	ba, wc, pr	none	–	ba, wc, pr	ba, wc, pr	ba, th	none	none
glaucescens	ba, wc, th, ch, pr	pr	pr	pr	pr	pr	wc	ba, wc, pr	–	ba, wc	pr	pr	wc, pr
hyperboreus	ba, wc, ch, pr	all patches	wc, pr	pr	ba, wc, pr	pr	ba, wc, pr	ba, wc, pr	ba, wc	–	wc, th, pr	ba, wc, pr	ba, wc, pr
michahelles	ba, wc, th, ch, pr	fo, th, ch	ch	none	none	fo, pr	none	ba, wc	ba, ch, pr	wc, pr	–	th	pr
occidentalis	ba, wc, th, ch, pr	fo, th, ch	fo, ch	pr	fo, ch	ba, wc, pr	none	ba, wc	ch, pr	ba, wc, pr	ba	–	none
marinus	all patches	wc	none	ba, wc	ba, wc	fo, ba, wc, pr	none	fo	wc, pr	fo, ba, wc, pr	ba, wc, ch	fo, ch, pr	–

might also help explain the potential difficulties of human visual identification of gull species based on plumage characteristics in the field.

Avian visual models of inter-specific differences in gull plumage colors revealed that most species are visually distinguishable in comparison with other gull species in at least one feather patch (Table 4). Many of these species-specific color differences match previous human visual perceptions. For example, feather coloration of the back and wings, which are often the focus of human descriptions of plumage differences between species, showed many inter-specific color differences based on avian visual models (Appendixes 2 and 3). Surprisingly, two feather patches that appear identical in coloration to previous assessments with human vision across all species were predicted to appear different to gulls across many species: the white forehead (Table 4, yellow highlight) and primary wing feathers (*see* Appendixes 2 and 3; 24.4% and 52.6% of male species comparisons, and 14.1% and 43.6% of female comparisons, respectively). We acknowledge that a 1.0 jnd threshold for discrimination of color stimuli is behaviorally supported in birds given very controlled experimental conditions (Kelber *et al*. 2003, Olsson *et al*. 2015), and more conservative thresholds (2–4 jnd) might be better estimates for many visual tasks in natural ecological settings (Siddiqi *et al*. 2004, Maia & White 2018), and/or to account for categorical perceptions of similar colors (Caves *et al*. 2018). Nonetheless, the 1.0 jnd threshold represents a criterion which generates testable hypotheses of color variation from an avian visual perspective. For example, the plumage color differences among closely related species that appear identical to humans, shown herein, represent potential unknown morphological divergence, and warrant more research from ecological and evolutionary perspectives (Benites *et al*. 2010, Wilson *et al*. 2012).

Contrasting with these examples of inter-specific color differences, we found a large number of inter-specific plumage color comparisons that were not above threshold for avian visual discrimination among gulls (Appendixes 2 and 3). In fact, 12 species pairs were indistinguishable from one another when comparing male plumage colors, and 24 species pairs when comparing female plumage colors (i.e., $\Delta S < 1.0$ for all feather patches; Table 4, red font). The similarities in plumage coloration and pattern among gull species might reflect recent evolutionary divergence and pervasive hybridization for many of our study taxa (Sonsthagen *et al*. 2016), and might suggest that traits (e.g., soft parts coloration, behaviors, etc.) other than plumage coloration are used by gulls to identify conspecifics. Gull similarities in appearance might also represent evolutionary constraint on plumage patterns and colors that facilitate countershading camouflage, or signaling efficacy for flocking or other gregarious behaviors, such as feeding or colonial nesting, in an open light environment (Gotmark 1987, Marchetti 1993, Thery 2006, Allen *et al*. 2012, Shultz & Burns 2013, Cuthill *et al*. 2016, Delhey 2019).

Extensive documentation of the differences between humans and birds in visual physiology and perception of color has called into question the ability of humans to interpret avian coloration, in general. Our results confirming gull plumages as sexually monochromatic superficially support studies that conclude a high correlation between humans and birds when assessing bird coloration differences on a course scale, such as levels of sexual dichromatism (e.g., Vorobyev *et al*. 1998, Armenta *et al*. 2008, Seddon *et al*. 2010, Bergeron & Fuller 2018). However, while spectrally distinct colors tend to be 'seen' as different colors by both birds and humans (Armenta *et al*. 2008, Håstad & Ödeen 2008, Seddon *et al*. 2010), there is generally large variation around the magnitude of color difference perceived, and in the subsequent interpretation of 'color difference' (Vorobyev *et al*. 1998, Håstad *et al*. 2005, Håstad & Ödeen 2008, Delhey *et al*. 2015). For example, Håstad & Ödeen (2008) found that human and avian modeling of feather colors identified different patches as the most contrasting within the same plumage of a given species. Furthermore, the lower bound of human visual discrimination of plumage colors is different from that modeled for birds (Vorobyev *et al*. 1998, Kelber *et al*. 2003), and behavioral responses confirm differences in these lower bounds (e.g., Sheldon *et al*. 1999, Mennill *et al*. 2003, Mays *et al*. 2004, Delhey *et al*. 2007). For instance, in our study the white forehead and primary wing feathers appeared identical in color to human vision, but avian visual models showed many inter-specific comparisons were above threshold for visual discrimination (*see* above), suggesting these patches can appear different, and species-specific, to gulls. Given these levels of hidden inter-specific color difference, and little hidden sexual dichromatism within species, our results emphasize the uncertainty of human vision to serve as a reliable proxy for avian vision.

Our results, as an example, highlight the ambiguities that exists for human visual assessments of plumage coloration: we confirmed human assessments of gulls as sexually monochromatic, but also found previously unknown potential morphological divergence in color among gull species in several plumage patches. Neither of these results were predictable *a priori*, given the widespread documentation of differences between human and bird assessments of coloration, particularly near the thresholds for discrimination in both taxa (e.g., Vorobyev *et al*. 1998, Mennill *et al*. 2003, Mays *et al*. 2004, Eaton 2005, 2007, Armenta *et al*. 2008, Håstad & Ödeen 2008, Seddon *et al*. 2010, Burns & Shultz 2012, Olsson *et al*. 2015, Hernández-Palma 2016, Bitton *et al*. 2017, Delhey *et al*. 2017). We reiterate the necessity for practitioners to collect objective reflectance data from feathers and quantify plumage colors with avian visual models when studying avian coloration, as differences between human and avian visual physiology make it impossible for humans to fully comprehend avian color space. We remain concerned by the continued interpretation of other types of data attempting to quantifying bird colors which cannot account for all color variation relevant to birds, potentially missing morphological divergence (e.g., Dale *et al*. 2015, Cooney *et al*. 2018, Cooney *et al*. 2019). Ultimately, our data and other similar studies, including those on other animals, can help properly focus and illuminate ecological, evolutionary, and behavioral questions related to coloration.

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Appendix 1. Plumage volume overlap between all *Larus* species pairs for both sexes (males lower diagonal, females upper diagonal). Values indicate proportions of volume (V) overlap between two species' plumages, measured as $V_{smallest} = V_{overlap}/V_{smallest}$ (thus, if one volume is entirely contained within the other, $V_{smallest} = 1$; Maia *et al.* 2013).

Larus species	*heermanni*	*delawarensis*	*canus*	*californicus*	*a. smithsonianus*	*thayerii*	*fuscus*	*dominicanus*	*glaucescens*	*hyperboreus*	*michahelles*	*occidentalis*	*marinus*
heermanni	–	0.193	0.885	0.314	0.511	0.304	0.244	0.402	0.193	0.319	0.301	0.631	0.176
delawarensis	0.045	–	0.570	0.972	0.294	0.254	0.715	0.561	0.696	0.590	0.978	0.471	0.681
canus	0.035	0.895	–	0.983	0.895	0.673	0.839	0.830	0.675	0.853	1	0.613	0.827
californicus	0.079	0.810	0.791	–	0.566	0.482	0.887	0.870	0.655	0.335	0.925	0.572	0.204
a. smithsonianus	0.166	0.765	0.933	0.925	–	0.624	0.279	0.587	0.485	0.631	0.697	0.307	0.214
thayerii	0.006	0.334	0.319	0.289	0.572	–	0.236	0.447	0.368	0.474	0.616	0.136	0.142
fuscus	0.223	0.458	0.794	0.948	0.608	0.420	–	0.553	0.587	0.629	0.993	0.795	0.808
dominicanus	0.227	0.639	0.798	0.965	0.804	0.557	0.683	–	0.661	0.653	0.997	0.581	0.468
glaucescens	0.013	0.580	0.639	0.407	0.833	0.612	0.722	0.742	–	0.610	0.725	0.290	0.192
hyperboreus	0.016	0.415	0.407	0.332	0.785	0.499	0.649	0.725	0.607	–	0.118	0.387	0.232
michahelles	0.028	0.924	0.928	0.796	0.999	0.270	0.978	0.999	0.261	0.069	–	0.912	0.235
occidentalis	0.107	0.874	0.908	0.855	0.974	0.164	0.968	0.949	0.401	0.035	0.475	–	0.833
marinus	0	0.538	0.228	0.070	0.234	0.046	0.586	0.104	0.159	0.089	0.003	0.086	–

Appendix 2. Avian perceptual color space distances (ΔS, in jnd) for all *Larus* male inter-specific comparisons for each plumage patch. Mean ΔS represents the average color space distance between all individual males for each of the two species compared, with the lower (lwr ΔS) and upper (upr ΔS) bounds of the 95% confidence interval around that mean, as calculated via bootstrap procedure (*see* Methods; Maia & White 2018). By definition, 1.0 jnd indicates threshold for visual discrimination of two colors, thus mean $\Delta S > 1.0$ with lwr $\Delta S > 1.0$ indicates evidence that male color of those species is distinguishable as different to gull vision for that plumage patch.

Larus species comparisons	forehead			back			wing coverts			throat			chest			primary		
	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS
a. smithsonianus/californicus	0.93	0.10	2.17	0.64	0.32	1.02	0.62	0.31	1.15	1.05	0.11	2.18	1.38	0.72	2.00	0.61	0.20	1.33
a. smithsonianus/canus	0.44	0.10	1.55	0.29	0.19	0.97	0.41	0.18	1.00	0.09	0.08	1.44	0.50	0.08	1.43	0.67	0.27	1.40
a. smithsonianus/delawarensis	1.13	0.28	2.14	0.28	0.05	0.89	0.19	0.06	0.91	1.02	0.18	2.02	0.72	0.09	1.66	0.15	0.08	1.27
a. smithsonianus/dominicanus	1.45	0.48	2.41	1.74	1.45	2.04	1.87	1.56	2.28	1.00	0.24	1.86	0.89	0.20	1.64	0.37	0.09	1.29
a. smithsonianus/fuscus	1.25	0.25	2.28	1.41	0.90	2.20	1.90	1.17	2.74	1.00	0.09	2.03	0.85	0.14	1.77	1.47	0.83	2.32
a. smithsonianus/glaucescens	0.45	0.16	1.67	0.34	0.13	0.69	0.23	0.04	0.73	0.76	0.09	1.97	0.09	0.09	0.75	1.92	1.71	2.31
a. smithsonianus/heermanni	2.64	1.61	3.65	3.90	3.40	4.38	3.19	2.80	3.63	3.22	2.04	4.25	1.98	1.60	2.45	2.54	1.66	3.52
a. smithsonianus/hyperboreus	1.78	0.61	2.93	1.86	1.22	2.39	1.86	1.15	2.51	1.64	0.46	2.71	1.26	0.55	1.96	3.10	2.82	3.57
a. smithsonianus/marinus	0.60	0.18	1.47	1.39	1.22	1.59	1.38	1.16	1.77	0.54	0.11	1.86	0.13	0.10	0.81	0.92	0.59	1.59
a. smithsonianus/michahellis	1.02	0.22	1.82	1.22	0.95	1.49	0.58	0.37	0.97	0.77	0.10	1.57	1.55	0.97	2.09	0.70	0.16	1.32
a. smithsonianus/occidentails	1.91	1.22	2.54	0.87	0.69	1.06	0.81	0.58	1.19	1.42	0.55	2.17	1.83	1.26	2.39	0.96	0.32	1.57
a. smithsonianus/thayerii	2.50	1.74	3.24	1.10	0.45	1.94	1.24	0.50	2.06	2.30	1.31	3.14	1.42	0.75	2.12	2.97	2.18	3.75
californicus/canus	1.35	0.15	2.68	0.53	0.06	1.24	0.83	0.30	1.37	1.09	0.16	2.35	1.88	1.19	2.66	1.02	0.51	1.58
californicus/delawarensis	2.04	0.81	3.37	0.87	0.32	1.51	0.71	0.22	1.37	2.07	1.07	3.20	2.09	1.22	2.84	0.51	0.22	1.49
californicus/dominicanus	0.53	0.08	1.76	1.40	1.17	1.67	1.44	1.19	1.77	0.21	0.13	1.12	0.50	0.10	1.01	0.92	0.37	1.56
californicus/fuscus	0.32	0.06	1.66	1.05	0.72	1.69	1.36	0.81	2.10	0.05	0.05	1.25	0.54	0.08	1.34	1.52	0.86	2.22
californicus/glaucescens	0.52	0.09	1.98	0.88	0.42	1.35	0.79	0.45	1.15	0.29	0.05	1.58	1.36	0.86	1.77	1.57	1.18	2.10
californicus/heermanni	1.72	0.48	2.96	3.26	2.73	3.80	2.58	2.21	2.99	2.18	1.07	3.32	1.37	1.23	1.60	2.92	2.25	3.65
californicus/hyperboreus	0.85	0.08	2.19	1.38	0.79	1.94	1.48	0.93	2.07	0.58	0.08	1.68	0.18	0.08	0.66	2.84	2.36	3.41
californicus/marinus	1.51	0.51	2.72	1.56	1.23	1.94	1.43	1.08	1.82	0.54	0.17	1.90	1.46	0.99	2.00	0.43	0.30	0.95
californicus/michahellis	0.11	0.09	1.37	0.58	0.30	0.96	0.07	0.05	0.46	0.28	0.07	1.28	0.18	0.04	0.53	1.26	0.81	1.64
californicus/occidentails	0.99	0.31	1.94	1.29	0.90	1.60	1.04	0.67	1.36	0.40	0.12	1.21	0.45	0.23	0.79	1.50	1.07	1.87
californicus/thayerii	1.58	0.47	2.59	0.62	0.18	1.49	0.83	0.32	1.57	1.25	0.39	2.15	0.14	0.09	0.57	3.38	2.76	4.03
canus/delawarensis	0.70	0.10	1.91	0.37	0.16	1.26	0.22	0.10	0.86	0.99	0.14	2.26	0.25	0.08	1.25	0.78	0.26	1.79
canus/dominicanus	1.87	0.75	2.93	1.46	1.21	1.85	1.75	1.34	2.24	1.05	0.29	2.11	1.38	0.60	2.29	0.42	0.17	0.96
canus/fuscus	1.67	0.42	2.87	1.13	0.64	1.99	1.88	1.03	2.77	1.04	0.11	2.26	1.34	0.34	2.29	0.90	0.31	1.77
canus/glaucescens	0.84	0.12	2.13	0.36	0.09	1.20	0.24	0.15	0.56	0.80	0.10	2.30	0.53	0.07	1.34	1.68	1.50	1.97
canus/heermanni	3.05	1.78	4.18	3.73	2.88	4.47	3.32	2.96	3.78	3.24	1.98	4.49	2.34	1.88	2.94	1.92	1.23	2.78
canus/hyperboreus	2.20	0.89	3.35	1.88	0.97	2.68	2.22	1.57	2.84	1.67	0.33	2.94	1.76	0.96	2.60	2.69	2.48	3.06
canus/marinus	0.17	0.07	1.14	1.18	0.84	1.83	1.02	0.85	1.25	0.56	0.08	2.04	0.44	0.10	1.26	1.21	0.55	1.88
canus/michahellis	1.43	0.43	2.37	1.10	0.32	1.68	0.77	0.43	1.17	0.81	0.07	1.80	2.05	1.40	2.76	0.50	0.40	0.77

continued

Appendix 2. Continued.

Larus species comparisons	forehead			back			wing coverts			throat			chest			primary		
	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS
canus/occidentails	2.31	1.46	3.15	0.78	0.22	1.60	0.42	0.32	0.64	1.45	0.42	2.41	2.32	1.67	3.02	0.63	0.49	0.92
canus/thayerii	2.92	1.99	3.78	1.11	0.29	2.07	1.58	0.92	2.40	2.34	1.20	3.38	1.91	1.19	2.68	2.37	1.70	3.06
delawarensis/dominicanus	2.57	1.56	3.63	1.76	1.45	2.18	1.82	1.46	2.33	2.00	1.30	2.70	1.60	0.72	2.41	0.51	0.10	1.61
delawarensis/fuscus	2.36	1.19	3.48	1.45	0.85	2.36	1.89	1.10	2.81	2.02	1.11	2.88	1.57	0.50	2.53	1.54	0.79	2.48
delawarensis/glaucescens	1.53	0.32	2.80	0.09	0.07	0.73	0.11	0.05	0.71	1.78	0.62	3.00	0.74	0.08	1.54	1.92	1.60	2.46
delawarensis/heermanni	3.74	2.74	4.82	4.10	3.43	4.78	3.26	2.73	3.84	4.23	3.28	5.13	2.59	1.95	3.22	2.67	1.57	3.86
delawarensis/hyperboreus	2.89	1.69	3.99	2.13	1.29	2.88	2.03	1.24	2.75	2.65	1.76	3.60	1.97	1.09	2.81	3.12	2.77	3.70
delawarensis/marinus	0.54	0.10	1.38	1.21	0.97	1.58	1.22	1.03	1.58	1.55	0.35	2.66	0.63	0.10	1.49	0.81	0.47	1.76
delawarensis/michahellis	2.12	1.29	3.00	1.45	0.90	1.98	0.66	0.26	1.19	1.79	1.03	2.50	2.27	1.48	3.00	0.84	0.17	1.79
delawarensis/occidentails	2.99	2.27	3.77	0.61	0.35	1.13	0.63	0.47	1.05	2.44	1.86	3.00	2.54	1.77	3.22	1.10	0.27	2.04
delawarensis/thayerii	3.62	2.86	4.40	1.37	0.48	2.32	1.40	0.61	2.32	3.31	2.62	3.99	2.12	1.24	2.97	3.11	1.99	4.15
dominicanus/fuscus	0.24	0.09	1.39	0.36	0.16	1.06	0.47	0.19	1.34	0.20	0.16	0.94	0.16	0.11	0.98	1.31	0.66	2.17
dominicanus/glaucescens	1.05	0.18	2.35	1.70	1.38	2.07	1.92	1.55	2.32	0.30	0.18	1.31	0.87	0.28	1.42	1.98	1.72	2.33
dominicanus/heermanni	1.26	0.48	2.30	2.94	2.34	3.51	2.08	1.51	2.79	2.30	1.53	3.17	1.51	1.35	1.73	2.19	1.38	3.20
dominicanus/hyperboreus	0.38	0.14	1.47	2.40	2.07	2.76	2.47	2.19	2.78	0.68	0.18	1.50	0.38	0.07	1.03	3.07	2.78	3.47
dominicanus/marinus	2.04	1.27	2.92	1.24	0.75	1.76	1.29	0.66	1.88	0.55	0.32	1.65	0.97	0.37	1.60	1.18	0.62	1.85
dominicanus/michahellis	0.49	0.13	1.32	1.40	1.23	1.59	1.42	1.16	1.73	0.30	0.12	0.89	0.67	0.21	1.11	0.34	0.10	0.88
dominicanus/occidentails	0.61	0.44	1.06	1.64	1.33	1.95	1.54	1.12	1.96	0.57	0.36	0.93	0.94	0.46	1.37	0.60	0.22	1.11
dominicanus/thayerii	1.06	0.37	1.71	1.85	1.54	2.36	1.96	1.68	2.39	1.32	0.75	1.87	0.53	0.08	1.13	2.61	1.84	3.43
fuscus/glaucescens	0.84	0.10	2.15	1.40	0.74	2.27	1.99	1.20	2.81	0.24	0.05	1.49	0.83	0.17	1.58	1.18	0.73	1.88
fuscus/heermanni	1.41	0.34	2.65	2.97	2.06	3.90	1.66	0.85	2.63	2.23	1.24	3.22	1.40	1.19	1.85	1.75	1.13	2.55
fuscus/hyperboreus	0.54	0.10	1.71	2.10	1.71	2.59	2.12	1.80	2.58	0.64	0.07	1.58	0.47	0.22	1.29	1.90	1.20	2.68
fuscus/marinus	1.82	0.81	2.79	1.18	0.53	2.09	1.64	0.68	2.54	0.49	0.12	1.79	0.94	0.20	1.76	1.52	0.83	2.21
fuscus/michahellis	0.25	0.09	1.15	1.08	0.87	1.53	1.36	0.78	2.11	0.23	0.04	1.08	0.71	0.14	1.44	1.35	0.66	2.17
fuscus/occidentails	0.70	0.26	1.54	1.43	0.67	2.30	1.76	0.90	2.59	0.45	0.18	1.12	0.98	0.25	1.73	1.38	0.69	2.18
fuscus/thayerii	1.26	0.49	2.16	1.51	1.10	2.20	1.69	1.32	2.28	1.30	0.50	2.11	0.61	0.24	1.42	2.25	1.68	2.94
glaucescens/heermanni	2.21	0.87	3.50	4.09	3.54	4.62	3.36	3.10	3.62	2.47	1.17	3.71	1.98	1.75	2.26	2.84	2.31	3.56
glaucescens/hyperboreus	1.36	0.15	2.70	2.18	1.53	2.71	2.08	1.49	2.58	0.88	0.08	2.14	1.24	0.68	1.78	1.29	0.81	2.09
glaucescens/marinus	0.99	0.09	2.19	1.13	0.95	1.36	1.26	1.15	1.42	0.26	0.10	1.73	0.12	0.04	0.68	1.48	1.18	2.01
glaucescens/michahellis	0.59	0.07	1.76	1.46	1.11	1.79	0.75	0.63	0.89	0.04	0.06	1.29	1.53	1.17	1.87	2.18	2.04	2.39
glaucescens/occidentails	1.47	0.46	2.48	0.54	0.38	0.81	0.67	0.62	0.72	0.67	0.16	1.64	1.80	1.43	2.14	2.27	2.14	2.46
glaucescens/thayerii	2.09	0.98	3.18	1.41	0.73	2.24	1.46	0.88	2.13	1.54	0.44	2.59	1.39	0.86	1.91	3.30	2.78	3.98
heermanni/hyperboreus	0.88	0.18	2.11	2.71	2.27	3.24	2.28	1.91	2.71	1.62	0.69	2.69	1.51	1.36	1.72	3.08	2.46	3.79
heermanni/marinus	3.20	2.32	4.15	4.14	3.49	4.76	3.28	2.74	3.84	2.68	1.44	4.10	2.09	1.80	2.47	3.05	2.36	3.88

continued

Appendix 2. Continued.

Larus species comparisons	forehead			back			wing coverts			throat			chest			primary		
	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS
heermanni/michahellis	1.63	0.78	2.59	2.70	2.22	3.15	2.61	2.38	2.83	2.46	1.62	3.27	1.36	1.15	1.60	1.92	1.25	2.86
heermanni/occidentails	0.75	0.09	1.56	4.33	3.85	4.81	3.32	3.01	3.70	1.80	1.07	2.52	1.40	1.19	1.64	1.70	1.05	2.68
heermanni/thayerii	0.43	0.36	1.09	3.03	2.46	3.67	2.32	1.99	2.73	1.08	0.58	1.86	1.51	1.36	1.72	0.51	0.25	1.37
hyperboreus/marinus	2.35	1.28	3.32	2.93	2.40	3.45	2.89	2.37	3.41	1.12	0.23	2.55	1.34	0.72	1.99	2.74	2.33	3.30
hyperboreus/michahellis	0.77	0.08	1.65	1.03	0.71	1.42	1.55	1.03	2.01	0.87	0.15	1.72	0.33	0.08	0.80	3.17	3.01	3.46
hyperboreus/occidentails	0.26	0.21	1.08	2.66	2.08	3.11	2.51	1.99	2.96	0.29	0.13	0.98	0.59	0.23	1.05	3.19	3.07	3.43
hyperboreus/thayerii	0.74	0.16	1.70	0.77	0.15	1.57	0.66	0.19	1.40	0.67	0.12	1.52	0.15	0.03	0.78	3.46	3.18	3.90
marinus/michahellis	1.58	0.93	2.25	1.97	1.70	2.26	1.37	1.09	1.66	0.26	0.11	1.66	1.63	1.25	2.14	1.50	0.94	1.96
marinus/occidentails	2.45	2.06	3.09	0.71	0.56	1.10	0.62	0.53	0.80	0.89	0.13	2.31	1.90	1.52	2.42	1.75	1.10	2.12
marinus/thayerii	3.08	2.60	3.65	2.18	1.65	2.98	2.24	1.67	2.94	1.79	0.80	3.08	1.49	0.92	2.10	3.54	2.84	4.27
michahellis/occidentails	0.90	0.56	1.23	1.83	1.73	1.93	0.97	0.88	1.07	0.66	0.41	0.97	0.27	0.22	0.36	0.29	0.28	0.39
michahellis/thayerii	1.50	1.03	2.02	0.51	0.48	1.04	0.89	0.36	1.59	1.54	0.89	2.16	0.21	0.08	0.56	2.33	1.78	2.94
occidentails/thayerii	0.75	0.57	0.99	1.88	1.29	2.68	1.85	1.30	2.50	0.94	0.55	1.30	0.45	0.18	0.80	2.08	1.57	2.67

Appendix 3. Avian perceptual color space distances (Δ*S*, in jnd) for all *Larus* female inter-specific comparisons for each plumage patch. Mean Δ*S* represents the average color space distance between all individual females for each of the two species compared, with the lower (lwr Δ*S*) and upper (upr Δ*S*) bounds of the 95% confidence interval around that mean, as calculated via bootstrap procedure (*see* Methods; Maia & White 2018). By definition, 1.0 jnd indicates threshold for visual discrimination of two colors, thus mean Δ*S* > 1.0 with lwr Δ*S* > 1.0 indicates evidence that female color of those species is distinguishable as different to gull vision for that plumage patch.

Larus species comparisons	forehead			back			wing coverts			throat			chest			primary		
	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS
a. smithsonianus/californicus	1.95	0.47	3.76	1.48	0.50	2.71	1.01	0.26	2.07	1.51	0.16	2.96	0.33	0.06	1.27	1.63	1.18	2.10
a. smithsonianus/canus	0.17	0.09	2.10	0.63	0.08	1.91	0.40	0.06	1.56	0.27	0.11	1.97	0.11	0.08	0.88	0.71	0.25	1.49
a. smithsonianus/delawarensis	2.31	0.72	4.21	1.16	0.16	2.65	1.35	0.28	2.53	1.93	0.64	3.36	1.60	0.58	2.63	2.05	1.34	2.83
a. smithsonianus/dominicanus	0.09	0.09	1.93	1.92	1.37	2.97	1.79	1.32	2.60	0.35	0.07	1.77	0.43	0.05	1.15	1.14	0.54	1.76
a. smithsonianus/fuscus	1.14	0.09	2.87	1.73	1.03	2.86	1.44	0.81	2.47	1.38	0.18	2.72	0.72	0.25	1.23	1.14	0.84	1.81
a. smithsonianus/glaucescens	2.05	0.36	4.02	1.68	0.61	2.96	1.80	0.74	2.96	1.44	0.17	3.00	1.01	0.36	1.75	2.46	2.10	2.99
a. smithsonianus/heermanni	1.32	0.19	2.90	1.92	1.27	2.82	2.20	1.38	3.18	0.28	0.07	1.92	1.36	1.18	1.62	1.17	0.73	1.88
a. smithsonianus/hyperboreus	0.36	0.14	2.19	0.45	0.23	1.29	0.33	0.25	1.26	0.28	0.07	1.73	0.56	0.10	1.29	3.01	2.90	3.18
a. smithsonianus/marinus	0.23	0.09	2.34	1.76	1.20	2.82	1.83	1.25	2.69	0.64	0.12	2.30	0.61	0.24	1.13	1.87	1.57	2.21
a. smithsonianus/michahellis	1.54	0.34	3.24	0.84	0.20	2.02	1.18	0.49	2.16	1.99	0.84	3.19	0.32	0.10	0.80	0.47	0.20	0.82

continued

Appendix 3. Continued.

Larus species comparisons	forehead			back			wing coverts			throat			chest			primary		
	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS
a. a. smithsonianus/occidentails	0.33	0.22	2.04	1.59	0.71	2.80	1.36	0.57	2.38	0.26	0.12	1.60	0.20	0.15	0.76	0.63	0.28	1.28
a. smithsonianus/thayerii	0.15	0.06	1.83	0.62	0.06	1.85	0.26	0.05	1.43	1.09	0.28	2.29	0.46	0.04	1.05	0.78	0.28	2.03
californicus/canus	2.09	0.89	3.31	0.85	0.19	1.53	0.62	0.13	1.32	1.74	0.36	3.18	0.27	0.07	1.30	1.00	0.26	1.90
californicus/delawarensis	0.40	0.10	1.55	0.34	0.14	1.45	0.47	0.22	1.14	0.43	0.05	1.59	1.27	0.23	2.54	0.68	0.33	1.40
californicus/dominicanus	1.92	0.99	2.86	0.93	0.75	1.25	1.05	0.83	1.32	1.19	0.16	2.29	0.77	0.10	1.69	0.51	0.08	1.18
californicus/fuscus	0.82	0.09	1.60	0.43	0.18	1.02	0.63	0.35	1.20	0.14	0.06	1.22	0.39	0.07	1.37	0.82	0.21	1.69
californicus/glaucescens	0.12	0.06	1.37	0.40	0.29	1.05	0.94	0.52	1.57	0.10	0.06	1.61	0.68	0.07	1.83	1.67	1.33	2.12
californicus/heermanni	3.25	2.21	4.26	2.81	1.88	3.76	2.71	2.02	3.55	1.78	0.40	3.15	1.30	1.12	1.74	2.39	1.63	3.28
californicus/hyperboreus	1.62	0.74	2.47	1.90	1.25	2.53	1.27	0.75	1.90	1.78	0.67	2.96	0.23	0.06	1.32	2.72	2.41	3.04
californicus/marinus	1.75	0.44	3.03	0.77	0.62	1.14	0.98	0.70	1.31	0.86	0.16	2.25	0.29	0.07	1.27	0.37	0.29	0.65
californicus/michahellis	0.45	0.18	1.03	0.65	0.11	1.19	0.18	0.08	0.48	0.48	0.05	1.37	0.07	0.07	0.97	1.26	0.94	1.65
californicus/occidentails	1.83	0.77	2.95	0.19	0.13	0.81	0.36	0.11	0.94	1.69	0.63	2.79	0.28	0.13	1.17	1.27	0.49	1.98
californicus/thayerii	2.10	1.25	3.02	0.89	0.34	1.54	0.78	0.31	1.40	2.59	1.62	3.54	0.79	0.11	1.67	2.32	1.18	3.63
canus/delawarensis	2.45	1.10	3.79	0.53	0.06	1.58	0.96	0.19	1.86	2.15	0.84	3.49	1.52	0.51	2.55	1.55	0.67	2.59
canus/dominicanus	0.25	0.12	1.45	1.41	1.14	1.71	1.50	1.19	1.98	0.61	0.20	1.82	0.51	0.11	1.20	0.58	0.18	1.61
canus/fuscus	1.29	0.25	2.41	1.13	0.77	1.60	1.12	0.71	1.78	1.62	0.43	2.86	0.65	0.13	1.30	0.45	0.18	1.40
canus/glaucescens	2.19	0.80	3.57	1.08	0.38	1.77	1.41	0.61	2.19	1.67	0.36	3.23	0.95	0.21	1.82	1.83	1.38	2.62
canus/heermanni	1.17	0.16	2.44	2.24	1.44	3.06	2.41	1.68	3.24	0.18	0.12	1.79	1.28	1.09	1.58	1.43	0.60	2.63
canus/hyperboreus	0.49	0.11	1.57	1.05	0.58	1.55	0.65	0.27	1.42	0.17	0.12	1.58	0.48	0.06	1.26	2.55	2.28	2.91
canus/marinus	0.40	0.17	1.97	1.23	1.00	1.60	1.50	1.10	2.01	0.88	0.13	2.52	0.54	0.13	1.19	1.23	0.52	2.07
canus/michahellis	1.67	0.65	2.63	0.24	0.11	0.61	0.80	0.34	1.37	2.21	1.09	3.38	0.24	0.03	0.85	0.57	0.38	1.17
canus/occidentails	0.36	0.16	1.63	0.97	0.44	1.52	0.98	0.41	1.71	0.07	0.07	1.62	0.10	0.07	0.82	0.31	0.13	1.33
canus/thayerii	0.09	0.08	1.30	0.14	0.09	0.66	0.16	0.06	0.98	0.90	0.24	2.01	0.52	0.09	1.14	1.33	0.20	2.85
delawarensis/dominicanus	2.28	1.15	3.46	1.14	0.95	1.76	1.30	1.18	1.56	1.62	0.69	2.50	2.03	1.01	3.06	0.97	0.31	1.90
delawarensis/fuscus	1.20	0.37	2.27	0.72	0.35	1.57	0.91	0.54	1.69	0.56	0.12	1.48	0.87	0.16	1.79	1.46	0.58	2.57
delawarensis/glaucescens	0.28	0.08	1.65	0.56	0.14	1.63	0.48	0.19	1.29	0.51	0.10	1.88	0.60	0.17	1.65	2.26	1.82	2.94
delawarensis/heermanni	3.59	2.35	4.81	2.64	1.59	3.77	3.18	2.35	4.10	2.21	0.88	3.48	1.63	1.08	2.49	2.97	2.06	4.04
delawarensis/hyperboreus	1.97	0.97	3.04	1.56	0.61	2.50	1.54	0.77	2.36	2.21	1.17	3.18	1.04	0.19	2.07	3.36	2.89	4.02
delawarensis/marinus	2.12	0.71	3.55	0.97	0.82	1.57	1.14	1.05	1.41	1.29	0.27	2.58	0.98	0.20	1.92	0.70	0.35	1.39
delawarensis/michahellis	0.77	0.09	1.75	0.37	0.12	1.25	0.47	0.38	0.99	0.06	0.03	0.86	1.28	0.38	2.18	1.61	0.99	2.34
delawarensis/occidentails	2.17	0.95	3.44	0.50	0.28	1.48	0.44	0.35	0.97	2.11	1.12	3.12	1.47	0.44	2.45	1.84	0.90	2.82
delawarensis/thayerii	2.46	1.44	3.62	0.55	0.15	1.54	1.09	0.33	1.90	3.02	2.15	3.82	2.04	1.04	3.04	2.81	1.59	4.18
dominicanus/fuscus	1.10	0.28	1.94	0.54	0.22	1.17	0.42	0.15	1.08	1.06	0.29	1.80	1.15	0.54	1.69	0.63	0.21	1.56
dominicanus/glaucescens	2.02	0.82	3.15	1.27	1.06	1.61	1.59	1.40	1.93	1.11	0.15	2.34	1.45	0.63	2.21	1.90	1.60	2.34

continued

Appendix 3. Continued.

Larus species comparisons	forehead			back			wing coverts			throat			chest			primary		
	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS	mean ΔS	lwr ΔS	upr ΔS
dominicanus/heermanni	1.38	0.39	2.43	2.54	1.74	3.37	2.55	2.10	3.23	0.61	0.08	1.84	1.54	1.21	1.97	2.00	1.24	2.89
dominicanus/hyperboreus	0.37	0.15	1.21	2.37	2.07	2.67	2.11	1.78	2.53	0.61	0.09	1.49	0.99	0.32	1.68	2.82	2.58	3.10
dominicanus/marinus	0.17	0.06	1.47	0.23	0.17	0.66	0.29	0.15	0.50	0.33	0.13	1.52	1.04	0.46	1.58	0.77	0.40	1.33
dominicanus/michahellis	1.51	0.84	2.18	1.18	1.08	1.30	0.90	0.78	1.04	1.67	1.12	2.24	0.75	0.17	1.24	0.75	0.30	1.27
dominicanus/occidentails	0.39	0.28	1.31	0.77	0.60	1.09	0.87	0.70	1.13	0.59	0.19	1.45	0.57	0.18	1.21	0.88	0.25	1.71
dominicanus/thayerii	0.20	0.08	1.09	1.52	1.34	1.78	1.65	1.37	2.06	1.41	0.71	2.07	0.07	0.05	0.73	1.86	0.70	3.17
fuscus/glaucescens	0.92	0.13	1.90	0.74	0.40	1.38	1.26	0.67	2.11	0.06	0.05	1.41	0.30	0.05	0.92	1.44	1.07	2.06
fuscus/heermanni	2.45	1.47	3.49	2.77	1.78	3.72	2.57	1.67	3.59	1.66	0.44	2.84	1.27	1.03	1.56	1.61	0.57	2.91
fuscus/hyperboreus	0.83	0.21	1.65	2.17	1.79	2.60	1.75	1.31	2.40	1.66	0.65	2.47	0.17	0.04	0.67	2.25	1.77	2.84
fuscus/marinus	0.93	0.08	2.18	0.40	0.17	1.06	0.40	0.21	1.05	0.74	0.15	1.91	0.12	0.03	0.45	0.96	0.31	1.87
fuscus/michahellis	0.46	0.21	0.89	0.90	0.72	1.21	0.48	0.23	1.12	0.61	0.19	1.19	0.41	0.22	0.61	0.98	0.67	1.51
fuscus/occidentails	1.07	0.32	2.10	0.25	0.09	0.82	0.48	0.19	1.24	1.58	0.70	2.43	0.62	0.17	1.07	0.58	0.21	1.55
fuscus/thayerii	1.29	0.59	2.14	1.21	0.96	1.63	1.27	0.89	1.86	2.47	1.73	3.07	1.17	0.76	1.59	1.67	0.61	3.07
glaucescens/heermanni	3.34	2.15	4.58	3.18	2.24	4.14	3.65	2.89	4.53	1.71	0.22	3.22	1.44	1.16	1.91	2.44	1.50	3.65
glaucescens/hyperboreus	1.72	0.59	2.85	2.06	1.43	2.70	1.94	1.16	2.75	1.71	0.40	3.06	0.47	0.08	1.16	1.15	0.67	2.02
glaucescens/marinus	1.85	0.33	3.27	1.12	0.94	1.53	1.38	1.26	1.64	0.79	0.14	2.37	0.42	0.06	1.04	1.69	1.36	2.21
glaucescens/michahellis	0.53	0.11	1.42	0.93	0.45	1.48	0.90	0.62	1.40	0.56	0.11	1.68	0.70	0.21	1.25	2.39	2.11	2.81
glaucescens/occidentails	1.92	0.61	3.17	0.51	0.41	0.96	0.80	0.56	1.42	1.63	0.44	2.99	0.92	0.31	1.63	1.88	1.39	2.64
glaucescens/thayerii	2.20	1.01	3.43	1.07	0.45	1.72	1.54	0.81	2.32	2.52	1.34	3.72	1.47	0.85	2.15	2.75	1.75	4.08
heermanni/hyperboreus	1.63	0.72	2.62	2.01	1.44	2.71	2.36	1.69	3.17	0.02	0.06	1.43	1.23	1.05	1.53	2.52	1.88	3.53
heermanni/marinus	1.55	0.23	2.98	2.51	1.66	3.37	2.79	2.32	3.42	0.92	0.21	2.33	1.22	0.94	1.55	2.56	1.80	3.55
heermanni/michahellis	2.82	2.05	3.62	2.29	1.54	3.02	2.76	2.22	3.45	2.26	1.20	3.34	1.25	1.06	1.44	1.58	1.09	2.26
heermanni/occidentails	1.43	0.40	2.62	2.81	1.94	3.68	2.91	2.18	3.71	0.24	0.16	1.43	1.19	1.01	1.42	1.13	0.38	2.33
heermanni/thayerii	1.18	0.23	2.12	2.33	1.55	3.10	2.38	1.70	3.24	0.81	0.18	1.90	1.51	1.26	1.83	0.65	0.36	1.89
hyperboreus/marinus	0.28	0.22	1.41	2.21	1.89	2.59	2.13	1.70	2.59	0.92	0.18	2.20	0.06	0.04	0.62	2.76	2.39	3.19
hyperboreus/michahellis	1.20	0.65	1.75	1.28	0.96	1.59	1.44	1.04	1.95	2.26	1.44	2.94	0.24	0.03	0.77	3.10	3.05	3.20
hyperboreus/occidentails	0.25	0.10	1.28	2.02	1.55	2.50	1.62	1.05	2.23	0.22	0.14	1.18	0.45	0.06	1.07	2.48	2.13	2.86
hyperboreus/thayerii	0.51	0.17	1.31	1.01	0.55	1.42	0.49	0.23	1.20	0.82	0.17	1.68	1.00	0.43	1.59	3.01	2.47	4.02
marinus/michahellis	1.35	0.53	2.24	1.01	0.98	1.14	0.81	0.69	0.95	1.34	0.62	2.14	0.30	0.24	0.44	1.49	1.40	1.62
marinus/occidentails	0.41	0.32	1.69	0.61	0.46	1.00	0.72	0.59	1.00	0.85	0.09	2.15	0.50	0.15	0.95	1.46	0.73	2.17
marinus/thayerii	0.37	0.10	1.67	1.34	1.20	1.62	1.66	1.30	2.09	1.73	0.74	2.76	1.06	0.67	1.45	2.54	1.50	3.82
michahellis/occidentails	1.40	0.54	2.30	0.75	0.38	1.13	0.19	0.07	0.66	2.17	1.47	2.83	0.23	0.06	0.62	0.68	0.41	1.14
michahellis/thayerii	1.69	1.18	2.36	0.34	0.23	0.62	0.95	0.61	1.49	3.07	2.72	3.43	0.76	0.40	1.12	1.26	0.58	2.38
occidentails/thayerii	0.42	0.24	1.43	1.03	0.61	1.49	1.14	0.62	1.83	0.96	0.38	1.67	0.57	0.20	1.11	1.10	0.26	2.52