Gloger's ecogeographical rule and colour variation among Willow Tits *Parus montanus*

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The Willow Tit *Parus montanus* is distributed across the Palaearctic and into the Oriental zoogeographical region with 15 subspecies. *P. m. borealis* is the only subspecies in Fennoscandia. Based on 86 skinned museum specimens from Norway (south of 64 °N), we found relatively large variations in the colours of the mantle, the underpart and the cheeks. Birds along the coast are significantly darker and have less white on their cheeks than inland birds. Furthermore, the birds become paler on their mantle, underparts and cheeks towards north and east, and in particular the annual precipitation explains a significant part of the colour variation. This is in accordance with Gloger's climatic rule that points out that feathers tend to be darkly coloured in habitats where relative humidity is high and pale where it is low.

Key words: Willow Tit; colour variation; Gloger's ecogeographical rule

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INTRODUCTION

The Willow Tit *Parus montanus* is a sedentary passerine bird with an extensive distribution across the Palaearctic and into the Oriental zoogeographical region (Cramp & Perrins 1993). The sexes are similar with no seasonal variation in plumage. Because of the highly sedentary nature of the species and its concentration in more or less isolated or montane regions, the subspecific taxonomy in Europe is complex (Hagemeijer & Blair 1997). On the other hand, as the geographical variation of the species is largely clinal, and because many subspecies intergrade widely, the species is sometimes considered possibly monotypic, with considerable variation within populations (del Hoyo *et al*. 2007). Altogether 15 subspecies of the Willow Tit have been described, differing generally in size, colour and song (del Hoyo *et al*. 2007). The eastern birds are in general larger and paler than the western birds, and the southern birds are smaller and darker than the northern ones (Harrap & Quinn 1996).

P. m. borealis is the only subspecies in Fennoscandia (Kvist *et al*. 2001). Based upon variation in colour, it has earlier been proposed to divide *borealis* into the subspecies *P. m. colletti* living in western Norway (Collett 1921, Haftorn 1971) and *P. m. lonnbergi* distributed in northern Scandinavia and northwestern Russia (del Hoyo *et al*. 2007). However, to our knowledge, the variation in plumage colour of the subspecies has not been quantified.

In this paper, we have analysed Willow Tits distributed in southern Norway to look for possible geographical variations in plumage colour and try to 1) quantify this variation, 2) see whether it varies clinally (gradually), and, if so, 3) see if the colour variation is related to climate or its correlates. According to Gloger's climatic rule (Gloger 1833, cited by Mayr 1963), birds and mammals tend to be dark in areas where relative humidity is high, and pale where it is low (Zink & Remsen 1986). The general association of dark colour and relatively high humidity is also found for beetles, flies and butterflies (Mayr 1963).

MATERIAL AND METHODS

The colours of 86 skinned museum specimens of adult Willow Tits sampled in southern Norway (south of 64 °N) were measured (Fig. 1).

For measuring we used the Munsell (1929) «Wall size 18-step neutral value scale»-chart to measure

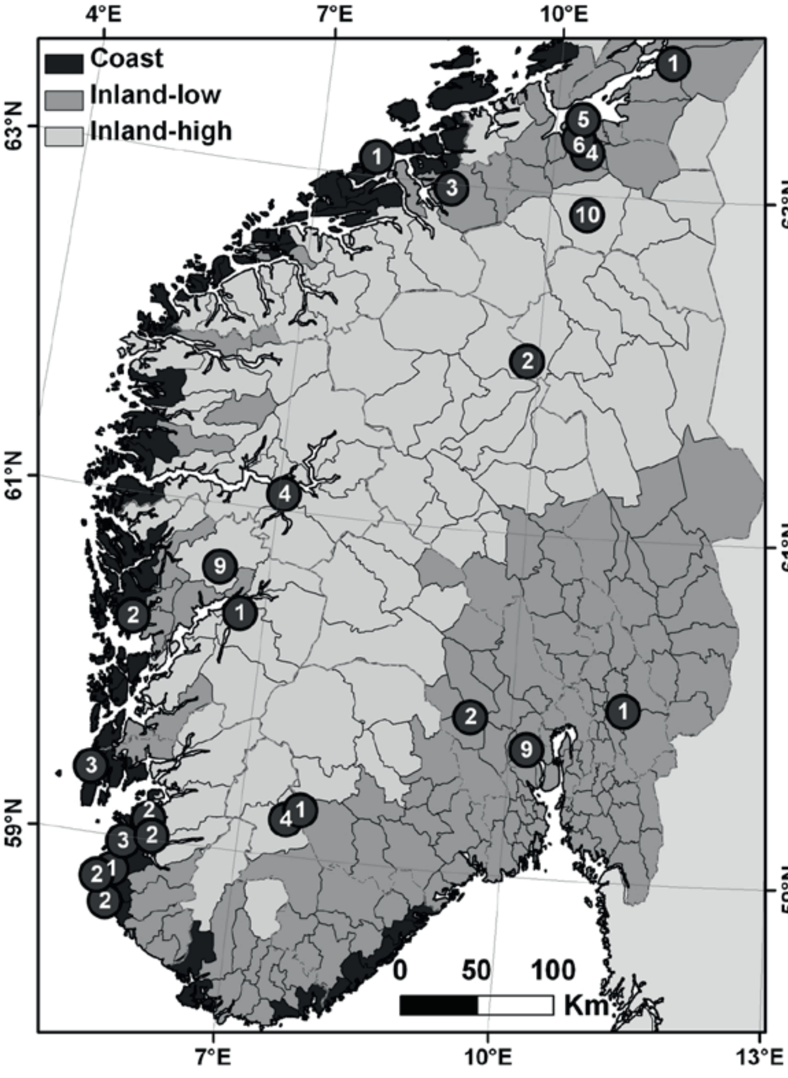

Figure 1. Map of southern Norway showing the sampling sites and the number of Willow Tits examined (figures in circles) in two simplified vegetation ecological regions, coast and inland. Based on Map 95 in Moen (1999).

the colour of the birds. These colour strips contain 18 steps arranged according to the percentage of reflection from black to white. The value notation indicates the degree of lightness or darkness of a colour in relation to a neutral grey scale which extends from theoretically pure black (0/) to theoretically pure white (10/), most often subdivided into 100 steps. Thus, a low figure indicates a darker colour than a higher figure. The chroma notation shows the strength or saturation of a colour, or its departure from a neutral grey of the same value. It extends from /0 for neutral grey up to /16, corresponding to the maximum saturation of the individual colour, i.e. brown-beige in the Willow Tit. Thus, a low figure indicates a greyer colour than a higher figure, which indicates a browner colour. All birds were scored by the same persons (OH and PGT).

The colour of the mantle, underpart, cheeks and cap were correlated with 1) the geographical position (latitude and longitude), and 2) maps (Moen 1999) of (a) vegetation ecological regions (mainly based on coast - inland); i.e. a combination of the demands of the plants for warmth in the growing season and differences in oceanity where atmospheric humidity and winter temperatures are important climatic factors; (b) the averages of annual temperature and amount of precipitation, each divided into 5 categories; (c) the growing season, i.e. the number of days with an average temperature of ≥5 ºC, being longest along the coast of west Norway, 220 days, and only 74 days at Finse (1222 m a.s.l.).

All tests are two-tailed, and were performed using SPSS 15. Data were analysed using nonparametric tests. Means are presented ± 1 SD.

Table 1. Mean values ± SD and coefficient of variation (CV=100SD/mean) in the colour variation of mantle, underpart, cheek and cap of 86 Willow Tits from southern Norway. The colour scale follows the Munsell scale (see Methods) where the notation denotes the degree of lightness or darkness from black (0) to white (10).

	Min	Max	mean ±SD	CV
Mantle	3.5	5.5	4.645 ±0.66	14.29
Underpart	5.0	8.5	7.11 ±0.72	10.14
Cheeks	6.5	9.0	7.90 ±0.57	7.19
Cap	1.5	2.0	1.52 ±0.11	6.95

RESULTS

Variation in plumage colour and colour patterns of the birds

The variation (coefficient of variation CV=100SD/mean) of the plumage colour of the birds is largest in the mantle and underpart, while the cheeks and cap vary less (Table 1). The chroma notation (saturation of the colour) is also higher for the mantle (CV=27.42) and the underpart (CV=31.80) than for the cheeks (CV=7.19) and the cap (CV=6.95). Thus, the plumage colour of the Willow Tits varies in the degree of lightness and the strength of saturation of the colour (greyish-brown).

*Table 2. Relationships (Spearman, r_s) between the colour of the mantle, underpart and cheeks of the Willow Tits (n=86). Figures in bold denote significant correlation values. **=p<0.01, ***=p<0.001*

	Underpart	Cheeks	Cap
Mantle	**0.49*** **	**0.30** **	0.07
Underpart	-	**0.62*** **	-0.07
Cheeks	-	-	-0.12

Birds with a pale mantle (high value) have a light underpart (r_s=0.49, p<0.001) and light cheeks (r_s=0.30, p=0.005; Table 2). The darkness of the cap shows no significant relationship with the colour of the mantle or underpart.

Variation in plumage colour and geographical sampling site of the birds

There were significant correlations between the latitude and the colour of the mantle, underpart and cheeks (r_s=0.41 to 0.56, p<0.001) and between the longitude and the colour of the mantle, underpart and cheeks (r_s=0.49 to 0.58, p<0.001), whereas no such relationship was found for the colour of the cap (r_s=-0.01 and 0.07). The chroma notation for the mantle and underpart is also higher towards the west (r_s=-0.33, p=0.002) and south (r_s=-0.27, p=0.012), showing that the birds are darker and browner in south-western Norway.

Figures 2 and 3 show the relationships between the clinal variation in the mantle colour and the latitude and longitude, respectively. These results reveal a clear relationship between a clinal variation in the colours of the Willow Tits and their sampling site, demonstrating that the birds are darker towards south and west than towards north and east. The east-west position of the Willow Tits therefore explains nearly 50% (R^2=0.47; Fig. 3) of the variation in the mantle colour of the birds.

Plumage colour of birds from coastal and inland areas

There is a significantly lower mean value of the colours of the mantle (4.14) and cheeks (7.61) of birds from coastal areas compared to those from inland areas (mantle 5.01, cheeks 7.99; Table 3), showing that birds from coastal areas have a darker mantle and less pale cheeks than inland birds. Although insignificantly so, the chroma notation for the underpart is lower for the coastal (1.31 ±0.35) than inland birds (1.64 ±0.48; Mann Whitney z=-1.19, p=0.23), indicating a slightly browner colour in coastal areas.

Plumage colour related to temperature, precipitation and growing season

The colour variations of mantle, underpart and cheeks are significantly correlated with the mean values of the annual temperature, amount of precipitation, and the length of growing season (r_s=-0.33 to -0.57, p<0.01), whereas the colour of

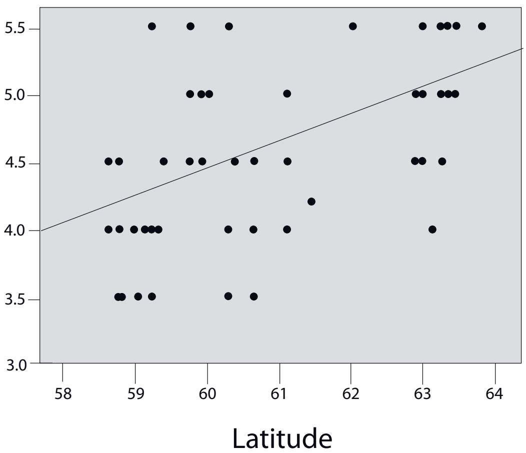

Figure 2. Relationship between the darkness of the mantle colour (the reflection values in Munsell notation; see Methods) of 86 Willow Tits and the latitude (°N) of sampling sites (r_s=0.56, p<0.001). A low figure indicates a darker colour than a higher figure. The slope of the linear regression, b_1=0.202.

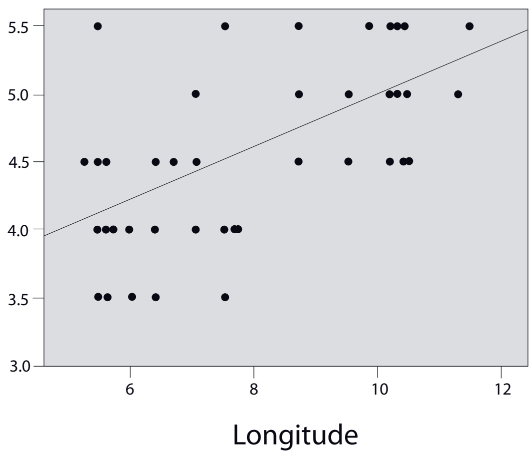

Figure 3. Relationship between the darkness of the mantle colour of the Willow Tits (n=86) and the longitude (°E) of sampling sites (r_s=0.58, p<0.001, b_1=0.215).

*Table 3. Mean values ± SD of the degree of darkness of the mantle, underpart, cheeks and cap of Willow Tits (n=86) caught in two vegetation ecological regions. A low value indicates a darker colour than a higher value. * denote statistical differences in a Mann Whitney test (2-tailed), *=p<0.05, **=p<0.01, ***=p<0.001.*

	Coast (n=18)	**Inland (n=68)**
Mantle	4.14 ± 0.38***	4.78 ± 0.66
Underpart	6.92 ± 0.49*	7.16 ± 0.77
Cheeks	7.61 ± 0.56**	7.98 ± 0.55
Cap	1.50 ± 0.00	1.53 ± 0.12

Table 4. Relationships (Spearman, r_s) between the colour variation in the plumage of the Willow Tit (n=86) and the mean annual precipitation and temperature and the length of the growing season.

	Annual precipitation	**Annual temperature**	**Growing season**
Mantle	**-0.57*** **	**-0.35*** **	-0.18
Underpart	**-0.46*** **	**-0.53*** **	**-0.38*** **
Cheeks	**-0.33** **	**-0.39*** **	**-0.32** **
Cap	-0.01	**-0.26***	**-0.26***

the cap is correlated only with the temperature and growing season (r_s=-0.26, p=0.016; Table 4). Since the annual temperature and precipitation and the growing season are significantly correlated with both latitude (r_s=-0.35 to -0.503, p<0.001) and longitude (r_s=-0.593 to -0.671, p<0.001), the results strengthen the suggestions that Willow Tits are darkest in the south-western areas where both the temperature and the amount of precipitation are highest.

Surprisingly, the mantle colour (r_s=-0.18, p=0.09) is not significantly correlated with the length of the growing season, whereas the colour of the underpart (r_s=-0.38, p<0.001, cheeks r_s=-0.32, p=0.003) and cap (r_s=-0.26, p=0.016) is.

The most significant relationships between the colour variations and the climatic parameters in Table 4 were found for the mantle, underpart and cheeks. The models obtained by univariate analysis of these variations (Table 5) confirm a significant contribution from the annual precipitation in explaining the colour variation for the mantle, underpart and cheeks. The annual temperature also gave a significant contribution in explaining the colour variation in the mantle, whereas the interaction between the precipitation and the temperature did the same for the cheeks. Altogether, these models explained 56 % of the colour variation for the mantle, and somewhat less (but still almost 40 %) for the underpart and cheeks.

To sum up, Willow Tits along the coast, especially in south-west Norway where the annual precipitation and temperature are relatively high, have significantly darker mantles and underparts and less white on their cheeks than those in inland areas where the annual precipitation and temperature are lower. This agrees with a clinal variation and with Gloger's rule.

DISCUSSION

The univariate analysis of variance using annual precipitation and temperature as predictors of the colour pattern shows that the average annual precipitation has particularly high predictive power. The Willow Tit plumage is darkest in the warmest, coastal areas, i.e. the most humid areas, and paler in the cool, dry inland areas, as predicted by the definition of Gloger's rule. This trend in the geographical variation in colour agrees with that reported in many other species (e.g. Hayes 2001). However, some exceptions can be found in the literature; for instance, the American Robin *Turdus migratorius* seems to follow a different pattern, being darker in the cool maritime forests of Newfoundland and paler in Mexico (Aldrich & James 1991).

The functional significance of such clinal variation in colour within species is not clear (Butcher & Rohwer 1989). A crucial question is how differences in colour are related to functional differences in various environments. The degree

Table 5. Results of univariate analysis of variance of plumage colour in Willow Tits (n=86). A full factorial model (F), including intercept and type III sum of squares (∑), is used. The categorised variables, annual precipitation (Prec.) and annual temperature (Temp.), are each divided into five steps. (Prec.: 1 = 500-700 mm, 2 = 700-1000 mm, 3 = 1000-1500mm, 4 = 1500-2000 mm and 5 = 2000-2500 mm; and Temp.: 1= 0-÷2°C, 2 = 2-0°C, 3 = 4-2°C, 4 = 6-4°C and 5 = 8-6°C)

Parameter	Source	Σ	df	F	p
Mantle	Corrected model*	20.85	10	9.43	< 0.001
	Prec.	2.23	3	10.10	< 0.001
	Temp.	1.48	3	6.69	< 0.001
	Prec. x Temp.	0.015	3	0.07	0.976
	*R^2 = 0.56				
Underpart	Corrected model*	1.74	10	4.85	< 0.001
	Prec.	1.59	3	4.45	0.006
	Temp.	0.73	3	2.05	0.114
	Prec. x Temp.	0.91	3	2.54	0.063
	*R^2 = 0.39				
Cheeks	Corrected model*	1.05	10	4.67	< 0.001
	Prec.	1.59	3	5.95	0.001
	Temp.	0.32	3	1.42	0.243
	Prec. x Temp.	1.56	3	6.94	< 0.001
	*R^2 = 0.38				

of melanism in animals has been related to physiological effects and it has been argued that colour is a selected trait because it may confer crypticity from predators (e.g. Greenberg & Droege 1990). On the other hand, it has been argued that dark feathers are more resistant than light feathers to bacterial degradation, which may be a problem in humid habitats where bacterial activity is high (Burtt & Ichida 2004).

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SAMMENDRAG

Gloger's klimaregel og fargevariasjon hos granmeis

Granmeis er utbredt over det mest av Europa og Russland og Sibir til Kamtsjatka-Japan med i alt 15 underarter. I Fennoskandia er *Parus montanus borealis* eneste underart. Basert på 86 skinnlagte museumseksemplarer av adulte meiser fra Sør-Norge (sør for 64 °N), viser det seg at rygg, underside og kinn av meiser varierer i lys-mørk farge. Fugler langs kysten er klart mørkere og har gråere kinn enn fugler fra innlandet, mens fuglene har lysere rygg, underside og kinn mot nord og øst. Det er forskjellene i årsnedbør som «forklarer» det meste av denne fargevariasjonen, men også temperaturen gir et signifikant bidrag til forklaringen av fargevariasjonen på ryggen. Dette er i overensstemmelse med Gloger's klimaregel som sier at fjærdrakten hos fugler er mørkest i områder med høy luftfuktighet og lysest i områder hvor luftfuktigheten er lav.

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