POPULATION DIFFERENTIATION AND ADAPTIVE SELECTION ON PLUMAGE COLOR DISTRIBUTIONS IN GYRFALCONS

JEFF A. JOHNSON[1] AND KURT K. BURNHAM[2]

[1]*University of North Texas, Department of Biological Sciences, Institute of Applied Sciences, 1155 Union Circle, #310559, Denton, TX 76203, USA*. E-mail: jajohnson@unt.edu

[2]*High Arctic Institute, 603 10th Avenue, Orion, IL 61273, USA*

ABSTRACT.—Extensive plumage color variation exists among Gyrfalcons (*Falco rusticolus*) throughout their circumpolar distribution, from white to silver, grey to brown and almost black. Multiple color variants do exist within some populations at differing frequencies; however, a few geographic locations possess a single predominate color variant. In northern Greenland and the high Arctic Canadian islands (>75°N), white Gyrfalcons prevail with the majority of adults possessing little if no barring on the retrices. Further south in western Greenland (66.5–67.5°N), silver and grey Gyrfalcons are also observed, whereas, in Iceland and some Eurasian populations, grey and dark grey to brown Gyrfalcons dominate, respectively. The above color pattern distributions are largely supported by population genetic differentiation measures based on neutral markers (i.e., microsatellite loci) identifying significant subdivision between Greenland and Iceland relative to other surveyed populations in north central Canada, Alaska, and Norway. In fact, within Greenland, asymmetric north to south dispersal patterns have been identified with genetic data. These distributional color patterns are also explained by allelic frequency distributions of the melanocortin-1 receptor (MC1R) gene, which has been identified as an important gene associated with hair and plumage color in some vertebrates. In Gyrfalcons, the white/melanic polymorphism in MC1R is perfectly associated with a fixed nonsynonymous point substitution. A single MC1R allele was observed in northern Greenland among white individuals, whereas further south an additional four alleles were observed among non-white individuals. Multiple MC1R alleles, including the "white" allele, were also observed in Canada, Alaska, and Iceland. However, no homozygous individuals for the "white" allele were observed in Iceland. Clearly, a significant geographic pattern exists relative to plumage color, and its distribution is supported by genetics. Multiple hypotheses are proposed to explain these patterns, such as directional selection based on crypsis and thermoregulation; however, ultimate mechanisms remain equivocal and require further study. These findings have important implications regarding a population's response to its environment and climate may be an important factor regulating Greenland Gyrfalcon plumage color distributions. To what extent similar patterns exist elsewhere in the species' distribution with regard to plumage color and reproduction is not known. *Received 1 March 2011, accepted 25 July 2011.*

JOHNSON, J. A., AND K. K. BURNHAM. 2011. Population differentiation and adaptive selection on plumage color distributions in Gyrfalcons. *In* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov (Eds.). Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho, USA. http://dx.doi.org/10.4080/gpcw.2011.0108

Key words: adaptation, dispersal, gene flow, MC1R, plumage color, population differentiation, reproductive success.

ANTHROPOGENIC ACTIVITIES continue to change our global natural environment in unprecedented ways (Vitousek et al. 1997) that have increased rates of population and species extinction to levels that our planet has not experienced for >70 million years, or since the last mass extinction. We have now entered the sixth mass extinction (Eldridge 2001). Many populations are struggling to adapt, and we have witnessed countless populations within our lifetime go extinct (e.g., Hughes et al. 1997). This loss of biodiversity is largely the result of habitat loss and fragmentation, which more recently has been exacerbated due to increasing rates of climate change (IPCC 2007). Many organisms are having difficulty adapting to their changing environment. This is especially true in the Arctic where biodiversity has been limited largely by its harsh environment. Today, arctic temperatures are now higher than at any time in the last 2,000 years (Kaufman et al. 2009). This in turn has influenced the arctic environment by influencing the distribution and abundances of its inhabitants (e.g., Parmesan 2006, Post et al. 2009). Consequently, an important question in the debate on the ecological effects of climate change is whether species will be able to adapt fast enough to keep up with their changing environment (Visser 2008). Therefore, how a population or species will respond to climate change will depend largely on its standing genetic variation, which is maintained depending on the effects of genetic drift or population size and created either by genetic mutation or immigration from neighboring populations. Because the rate of change associated with current climate change is high, mutation is likely to play a much smaller role in generating or maintaining population genetic variability compared to dispersal patterns. Possessing basic information on overall connectivity between populations is crucial for predicting how a species may change over time.

For the Gyrfalcon (*Falco rusticolus*), limited information is available concerning overall population connectivity throughout its circumpolar arctic and sub-arctic distribution. Latitudinal breeding range for Gyrfalcons extends as far north as 82°N in Peary Land, Greenland, to 54°N on the Kamchatka Peninsula in Russia and Hudson Bay in Canada, with populations generally distributed across six areas: Alaska, Canada, Greenland, Iceland, Fennoscandia, and Siberia (Koch 1925, Johnsen 1953, Cade 1982, Potapov and Sale 2005). Although, subspecies designations are not currently recognized for Gyrfalcons, historically this species has been described as polytypic with as many as 40 different subspecies (Vaurie 1961, Snow 1974, Cade et al. 1998, Potapov and Sale 2005).

Taxonomic designations used most often in the past consist of five to seven subspecies largely based on plumage color (see Figure 1). Gyrfalcons from northern Greenland and northeastern Canada are largely white and white to semi-white or silver, respectively (i.e., *candicans*); those from mid- to southern Greenland and North America are semi-white or silver to grey to dark grey or black (i.e., *obsoletus*); those from Iceland are light grey to grey (i.e., *islandus*); in Fennoscandia and Russia they are mostly grey (i.e., *rusticolus*); and in Siberia they are typically grey to light grey or white (i.e., *intermedius, uralensis, grebnitzkii*). These characters, however, do not strictly conform to geography, with each "color morph," or "variant," occurring in many of the same areas (Todd and Friedmann 1947, Vaurie 1961, Ellis et al. 1992, Cade et al. 1998, Flann 2003, Potapov and Sale 2005), and multiple variants have been observed among offspring within the same nest (Todd and Friedmann 1947, White and Cade, 1971, K. Burnham, unpub. data). However, there are geographic areas such as northern Greenland and Iceland that do

Figure 1. Gyrfalcon color variants.

have a high percentage of a single color variant observed among breeding individuals' suggesting that selection or drift through vicariance may influence plumage color distribution.

Here, we first discuss the degree of population genetic differentiation or connectivity, that exists among Gyrfalcon populations throughout their circumpolar distribution. Given the wide range of Gyrfalcon color variants and their geographic distribution, one might expect Gyrfalcon dispersal patterns to reflect various degrees of connectivity between populations. For example, geographic areas that possess a single color variant at high frequency are populations that are more likely to possess limited or no immigration, e.g., Iceland and northern Greenland. Second, after establishing the degree of connectivity among Gyrfalcon populations, we then explore potential mechanisms that may influence plumage color distribution, specifically, the interaction between genetics (or genotype) and plumage color (or phenotype) and the selective forces that may drive its variation (Roulin 2004). By understanding the link between genotype and phenotype for ecologically important traits such as plumage color, we can better predict how future changes in climate may affect Gyrfalcon populations (Winker 2009, Hoffmann and Sgró 2011).

Gyrfalcon Population Connectivity

In a recent study investigating levels of genetic differentiation among Gyrfalcon populations using nuclear microsatellite loci, Johnson et al. (2007) documented significant structure, or reduced connectivity, among sampled locations in both Greenland and Iceland relative to other areas in north central Canada, Alaska and Norway (Figure 2). In contrast, limited differentiation was observed between sampled areas in Canada, Alaska, and Norway, suggesting that one large population exists across the Canadian Arctic, through Alaska and Siberia to northern Scandinavia. Although, genetic data do not exist from samples collected in Russia to confirm connectivity between Alaska and Scandinavia, these results are supported by satellite telemetry data. McIntyre et al. (2009) have documented movements of juvenile Gyrfalcons from Alaska to Russia, and similar patterns have also been observed in the Snowy Owl (*Bubo scandiacus,* Fuller et al. 2003), a species that possesses similar ecology and life history constraints to the Gyrfalcon. Further, Marthinsen et al. (2009) documented no genetic signal suggesting population differentiation between Snowy Owl population samples collected in eastern Siberia and North America using mitochondrial DNA control region sequence data.

In contrast, both Greenland and Iceland populations appear isolated with respect to other sampled populations. Using satellite telemetry, Burnham (2008) and Burnham and Newton (2011) observed high breeding season philopatry with Gyrfalcons in Greenland. Similarly, within Iceland, no white Gyrfalcons during the breeding season have been observed, only grey Gyrfalcons (O. Nielsen, pers comm.). This suggests limited or no immigration to Iceland since eastern Greenland is the likely source of individuals, most of which are predominately white in plumage color (K. Burnham, unpubl. data). The genetics data in Johnson et al. (2007) certainly support this conclusion with significant differentiation observed for both Greenland and Iceland Gyrfalcon populations.

Within Greenland, an obvious latitudinal difference exists with respect to plumage color distributions. White Gyrfalcons with little barring pattern predominate in northern Greenland, with only a single grey female and her chick observed from over 170 recorded Gyrfalcon sightings in the Thule study area (75.9–77.6° N) between 1993 and 2005 (Burnham 2008). Similarly, over a two-year period, Gyrfalcons were sampled on autumn migration in eastern Greenland near Scoresbysund (70.4° N), and all but two (n=125 trapped) possessed white plumage (Burnham 2008). In the Kangerlussuaq study site (66.5–67.5° N) in western Greenland, approximately 1,170 km south of Thule, multiple plumage color variants exist. Between 1998 and 2005, Burnham (2008) documented 58 (52%) white, 14 (13%) silver, and 40 (36%) grey Gyrfalcons. No obvious pairings based on plumage color were observed, with mixed pairings as frequent as those between similar color variants (K. Burnham, unpubl. data). Using nuclear microsatellite DNA, Johnson et al. (2007) documented asymmetric dispersal patterns within Greenland with Gyrfalcons dispersing south from Thule to Kangerlussuaq, yet no signal was observed suggesting dispersal in the opposite direction. These data agree with the observed plumage color distributions, further supporting a possible proximate mechanism for maintaining the predominant white variant in the extreme north.

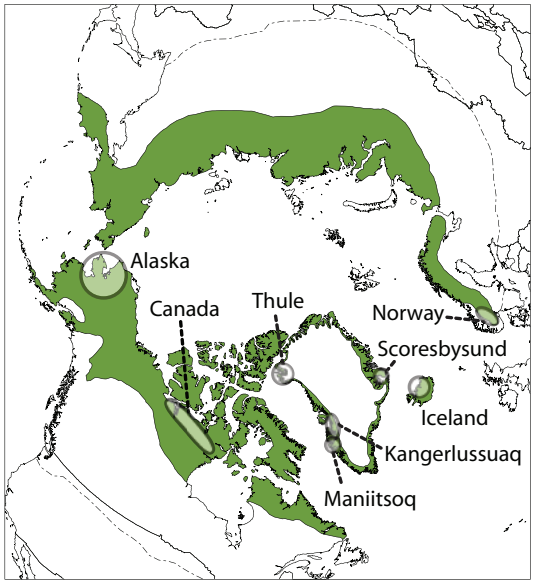

Figure 2. Geographic breeding distribution of Gyrfalcons. Sampling locations are shown with the size of each ellipse representing the approximate geographic area sampled.

GENETICS OF PLUMAGE COLOR

To predict how populations may respond to changes in the environment given a specific phenotype, e.g., plumage color, and how they may evolve under varying selection, trait heritability of that phenotype is required. Multiple studies have been conducted recently focused on the genetics associated with coat (mammals, Hoekstra 2006) and plumage (birds, Mundy 2006) color variability in vertebrates. Although over 100 genes have been linked to coat color in laboratory mice (Bennett and Lamoreux 2003, Hubbard et al. 2010), one gene that has received considerable attention with respect to melanin-based coloration is the melanocortin-1 receptor gene (MC1R). MC1R is a key protein involved in regulating melanin synthesis for deposition in specialized pigment cells called melanocytes during tissue develop-

ment, and has been identified as an important gene associated with hair and plumage color in some vertebrates.

For example, MC1R appears to control qualitatively different plumage color patterns with respect to melanin in multiple distantly related bird species, the Bananaquit (*Coereba flaveola,* Theron et al. 2001), Lesser Snow Geese (*Anser caerulescens caerulescens*) and Parasitic Jaeger (*Stercoarius parasiticus,* Mundy et al. 2004), Japanese Quail (*Coturnix japonica,* Nadeau et al. 2006), Red-footed Boobies (*Sula sula,* Baião et al. 2007), swans (*Cygnus* spp., Pointer and Mundy 2008), flycatchers (*Monarcha castaneiventris,* Uy et al. 2009), Eleonora's Falcon (*Falco eleonorae,* Gangoso et al. 2011), and domestic chickens (Kerje et al. 2003, Ling et al. 2003). Plumage coloration in each of these species has a strong correlation with particular MC1R genotypes differing by nonsynonymous substitutions resulting in amino acid and presumably protein structural differences following translation (see also Mundy 2005). In other cases, MC1R genetic variability is not correlated with plumage color (Blue-crowned Manakin, *Lepidothrix coronata,* Cheviron et al. 2006, fairy wren spp., Driskell et al. 2010, Red-tailed Hawk, *Buteo jamaicensis,* Hull et al. 2010, Willow Grouse, *Lagopus lagopus,* Skoglund and Höglund 2010). Although the actual mechanism in birds by which nonsynonymous substitutions in MC1R affect melanin synthesis is not fully understood (Ling et al. 2003, McGraw 2006), studies in mammals (García-Barron et al. 2005) and reptiles (Rosenblum et al. 2010) have identified altered functional properties specific to certain MC1R allelic variants. In the Beach Mouse (*Peromyscus polionotus*), for example, Hoekstra et al. (2007) have identified multiple nonsynonymous point substitutions in the coding region of MC1R that alter protein function and influence the degree of signaling activity associated with the production of dark pigmentation in hair.

Using Gyrfalcon samples that were used in the microsatellite study described above (with the exception of Norway), Johnson et al. (2012) identified six nucleotide substitutions in the coding region of MC1R that resulted in nine alleles (Figure 3). The nine alleles differed in their overall geographic distribution with at least two MC1R alleles observed in almost all sampled populations. Scoresbysund in northeastern Greenland possessed a single allele. Similarly, all individuals sampled in Thule, with the exception of one female grey Gyrfalcon, were homozygous for the same allele observed in Scoresbysund (Figure 3). Multiple alleles at MC1R were observed in populations with plumage color variation, specifically, non-white individuals. The Kangerlussuaq population possessed five alleles and Iceland possessed the highest number with seven alleles.

Of the six observed nucleotide substitutions in MC1R, three resulted in amino acid substitutions (i.e., nonsynonymous): valine to isoleucine at amino acid position 130 ($Val^{130}Ile$), arginine to cysteine at amino acid position 144 ($Arg^{144}Cys$), and threonine to isoleucine at amino acid position 263 ($Thr^{263}Ile$). When comparing the three nonsynonymous substitutions with individual Gyrfalcons from which we possessed plumage color information, we identified a single nucleotide substitution at nucleotide 268 resulting in an amino acid variant $Val^{130}Ile$ that was perfectly associated with 'white' vs 'non-white' variants (Figure 4). This distinction was further supported with Gyrfalcons from northern Greenland (Thule and Scoresbysund) where the majority of birds sampled where white color variants. With the exception of one grey female in Thule, all Gyrfalcons in northern Greenland were homozygous for the 'white' allele (val^{130}), while the grey female was heterozygous at this position ($Val^{130}Ile$). In both central-west Greenland (Kangerlussuaq) and Alaska, where we possessed plumage color information on sampled Gyrfalcons, heterozygous $Val^{130}Ile$ individuals were either silver or

Figure 3. Nine MC1R alleles observed among Gyrfalcons populations. Vertical numbers indicate the positions of variable nucleotides within 729 bp of sequence. The three vertical grey columns indicate the three nonsynonymous nucleotide substitutions. Dots under nucleotide positions indicate an identical nucleotide as given with allele 1.

							Greenland					
	268	300	310	648	668	696	Thule	Kanger.	Scoresby.	Iceland	Canada	Alaska
allele 1	G	C	C	G	T	C	63	44	60	10	8	18
allele 2	A	T	.	A	.	.	1	7	-	18	2	12
allele 3	A	.	.	.	.	.	-	6	-	12	7	9
allele 4	A	.	T	.	.	.	-	-	-	-	-	1
allele 5	A	.	.	A	C	.	-	-	-	1	3	-
allele 6	A	.	.	.	.	.	-	5	-	1	-	-
allele 7	A	T	.	.	.	.	-	-	-	1	-	-
allele 8	A	T	.	.	.	T	-	-	-	1	-	-
allele 9	.	.	.	.	C	.	-	2	-	-	-	-

grey in plumage color (Figure 4). Although we do not have plumage color information to confirm, two out of ten (20%) Gyrfalcons sampled in north central Canada were homozygous for the 'white' allele. Interestingly, the 'white' allele was also observed in Iceland where only grey Gyrfalcons are observed during the breeding season (O. Nielsen, pers. comm.). Out of the 22 Gyrfalcons from Iceland, ten possessed the 'white' allele (45%), but they were all heterozygous.

Therefore, based on the individual Gyrfalcons that were sampled, of which we possessed plumage color information, including Gyrfalcons from northern Greenland that are predominately white, a nonsynonymous point substitution ($Val^{130}Ile$) in the MC1R gene was found to be perfectly associated with color variation with respect to 'white' vs 'non-white' individuals. These results suggest that the MC1R follows a Mendelian dominance inheritance pattern with respect to melanin production in developing feathers. A recent study investigating inheritance of plumage color variants including banding patterns in captive Gyrfalcons also supports this finding. Chang et al. (2010) concluded that plumage color observed within a captive Gyrfalcon population was best described by an inheritance pattern based on two genes, one gene involved in pigment production following Mendelian dominance inheritance and another gene, most likely codominant, controlling actual pigment deposition that would influence marking pattern on feathers. A second gene or multiple genes may control marking pattern and melanin deposition in individuals capable of melanin production (i.e., heterozygous and homozygous dominant MC1R genotypes, Chang et al. 2010). When a gene such as MC1R is homozygous recessive, pigment production would not occur, thereby making the genotype at loci controlling pigment deposition irrelevant (Chang et al. 2010).

However, 'white' Gyrfalcons possess a small degree of marking, particularly on the tips of primaries, despite a homozygous recessive MC1R genotype. If MC1R homozygous recessive individuals do not produce melanin, then how would a second gene associated with pigment deposition influence 'white' Gyrfalcons? A second gene, therefore, likely influences melanin production associated with marking pattern. For example, an additional gene may be more involved with the up-regulation of extracellular alpha melanin-stimulating hor-

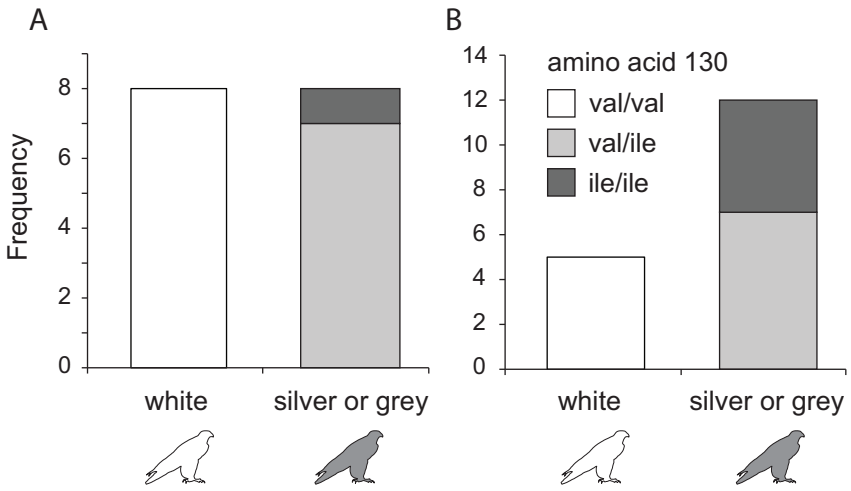

Figure 4. Frequency of MC1R genotypes and Gyrfalcon plumage color phenotypes at (A) Kangerlussuaq, Greenland (n=16) and (B) Alaska, USA (n=17).

mone (α-MSH), which could produce continuous variation in the level of melanism during pigment deposition as shown with vertebrates other than birds (Rasmussen et al. 1999, but see Takeuchi et al. 2003), which could then be regulated by multiple genes influenced by other factors in the genome (i.e., epistasis, Steiner et al. 2007, Pointer and Mundy 2008, Hubbard et al. 2010). More work is required to identify additional gene(s) associated not only with the regulation of melanin production, but also genes that influence marking pattern in Gyrfalcons (see also Potopov and Sale 2005, chapter 2). Genetic analyses with a larger number of silver and grey Gyrfalcon samples with varying degrees of marking pattern and a detailed pedigree will be necessary to discern these relationships in greater detail.

Adaptive Significance of Plumage Color

The distribution of color traits among vertebrates is often under the control of selection because even small changes in color can have a dramatic effect on an individual's ability to survive or reproduce (e.g., Bortolotti et al. 2008, Anderson et al. 2009, Gasparini et al. 2009, Mullen et al. 2009, Jacquin et al. 2011). The actual mechanism can vary depending on the species and environment (Roulin 2004), and many questions remain unresolved concerning the maintenance of plumage color and pattern differences among birds (Brooke 2010, Gluckman and Cardoso 2010). This is certainly the case with Gyrfalcons, with no experimental data existing that focuses on how selection may influence plumage color distribution in this species. The role of selection with regard to plumage color is of importance for predicting how Gyrfalcon populations may respond to future environmental changes.

Alternatively, the patterns we observe with respect to plumage color distribution may also be the result of historic processes associated with genetic drift and extended periods of allopatry among glacial refugia (Hewitt 1996, Newton 2003, Stewart at al. 2010). The occupancy of separate "closed" ice-free refugia during glacial periods, for example, would allow divergence among taxa and the accumulation of unique traits through selection and/or drift. During the time period covering the last glacial maximum (~26–14 thousand years ago)—the Wisconsin in North America and the Weichselian in Eurasia—a number of northern latitude closed refugia have been proposed. Northern refugia may have existed in northern Greenland (Peary Land), in northern (Banks Island) and eastern Canada (Gaspé Peninsula and Newfoundland), in northwest Iceland, and in northwestern Norway; however, results have

been inconclusive concerning their overall contribution to divergence among taxa, let alone their existence based on geological evidence (Dahl 1955, Ploeger 1968, Salomonsen 1972, Buckland and Dugmore 1991, Pielou 1991, Andersen and Borns 1994, Bennike 1999, Stewart and Lister 2001, Newton 2003, Ægisdóttir and Þórhallsdóttir 2004, Provan and Bennett 2008). In contrast, a large ice-free area (Beringia) extending from Alaska over the Bering land bridge into eastern Siberia has been well documented (Pielou 1991, Andersen and Borns 1994, Abbot and Brochmann 2003, Newton 2003, Hewitt 2004). As a result, a number of recent studies have used a glacial vicariance hypothesis and the occupancy of northern refugia during the last glacial maximum to help explain the distribution of genetic diversity observed in many extant populations, especially those in the arctic and sub-arctic regions (see refs in Provan and Bennett 2008).

The presence of geographic structure among Gyrfalcon sampling locations that corresponds to phylogeographic patterns observed with some co-distributed arctic and sub-arctic taxa suggest that this species' current distribution may have been influenced by the presence of multiple glacial refugia during the last glacial maximum (Holder et al. 1999, Fedorov and Stenseth 2002, Brunhoff et al. 2003, Waltari et al. 2004, Walteri and Cook 2005). The majority of these studies have used mtDNA divergence estimates to assess correspondence with timing of glacial activity; however, the low mtDNA variability among Gyrfalcons (Johnson et al. 2007) and the lack of supporting information pertaining to a good geological calibration make it difficult to obtain estimates for their population divergences.

Consequently, our current data do not allow us to address whether Gyrfalcons occupied multiple glacial refugia during the last glacial maximum. However, we can address how contemporary disruptive or directional selection may influence plumage variation among Gyrfalcon populations where gene flow currently exists, particularly within Greenland. If the current distribution of color variants were due to drift alone, how can one explain the asymmetric dispersal pattern from north to south observed within Greenland today (Johnson et al. 2007)? In this case, selection may play a role with regard to contemporary plumage color distribution in Gyrfalcons. For example, disruptive selection is often associated with a variable environment, either spatially or temporally, and favors extreme individuals given a normally distributed population for a particular trait such a plumage color. The trait(s) that determine the fittest phenotype may vary geographically where 'white' plumage has the highest fitness in one habitat type and 'grey' plumage in another type. These traits could also vary temporally within a geographic location depending on the standing genetic variation and the degree of environmental heterogeneity, with selection influencing the frequency of each phenotype in a population. The strength of selection will dictate to what degree variation is maintained in a given population, with strong directional selection often resulting in fixation of a particular trait depending on the degree of introgression from neighboring populations (Roulin 2004).

Possible mechanisms influencing plumage color distribution in birds through selection range from crypsis, thermoregulation, advertisement, vision enhancement, and plumage protection from abrasion or bacterial degradation (see Bortolotti 2006). Alternatively, plumage color variation in Gyrfalcons may also be selectively neutral, but as described above, a variable environment may also promote and maintain plumage color variations depending on how fitness or reproductive success varies between years. Tickell (2003) has suggested that white may be the 'default' plumage color in birds, particularly among waterbirds. If no selective advantage exists for possessing colored plumage, then selection provides no mechanism to maintain pigmentation. Therefore, by not producing pigment, a white bird may then utilize that energy for

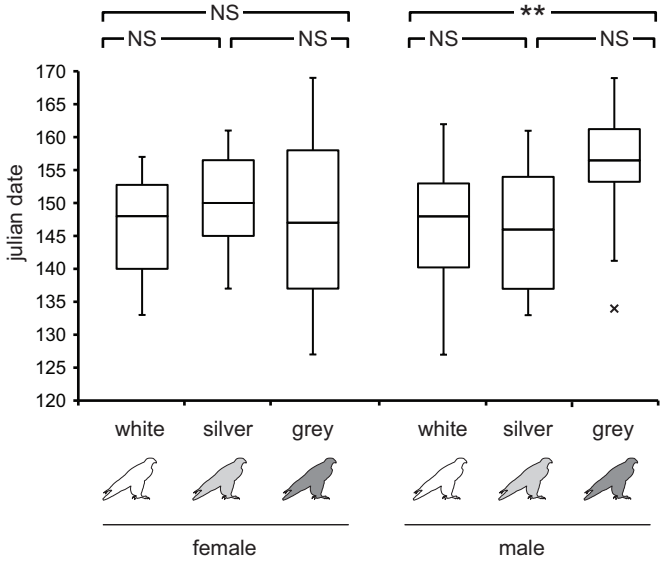

Figure 5. Hatch date for female (n=66) and male (n=51) nests based on plumage color (Kangerlussuaq, Greenland). Box plots show medians and quartiles (x = minimum outlier; NS = not significant, P>0.05; ** = P< 0.01).

other purposes. Here, we explore whether factors such as crypsis or thermoregulation may influence Gyrfalcon plumage color distribution in Greenland.

It is not known whether plumage color provides any benefit or significant cost to Gyrfalcons. However, data do suggest that the timing of nest initiation and egg-lay-date covaries with plumage coloration. In central-west Greenland near Kangerlussuaq, where multiple plumage variants exist from white to silver to grey, Johnson and Burnham (in review) observed a significant difference in offspring hatch date at nests that possessed either white or grey males (Mann-Whitney test, Z = –2.72, P = 0.007). Nests of white males had significantly earlier hatch dates (median julian date = 147.0, range = 126–161, n = 34) than grey males (median = 155.5, range = 133–168, n=10; Figure 5), or a difference of 8.5 days between median hatch dates. Although hatch dates for silver male nests (median = 145, range = 132–160, n = 7) were similar to white male nests (Z = –0.23, P = 0.82), results suggest a marginally non-significant difference between silver and grey male nests (Z = –1.76, P = 0.08). In contrast, no significant difference existed between female Gyrfalcons based on plumage color and hatch date at nests with white females (median = 147.0, range = 132–156, n = 26) being similar to silver (median = 149.0, range = 136–160, n = 15; Z = –1.61, P = 0.11) and grey females (median = 146.0, range = 126–168, n = 25; Z = 0.60, P = 0.55) and silver similar to grey females (Z = –0.62, P = 0.54; Figure 5).

When comparing hatch date and plumage color of both male and female nest site pairs in the Kangerlussuaq population, egg hatch date differed (Z = –2.78, P = 0.005) with white-white pairs (median = 149.5, range = 132–156, n = 18) earlier than grey-grey and silver-grey pairs combined (median = 155.5, range = 132–168, n = 12; Johnson and Burnham in review). Although the sample sizes for grey-grey (median = 161.0, range = 154–168, n = 5) and silver-grey (median = 152.0, range = 132–160, n = 7) paired individuals were small, grey-grey pairs nested later than silver-grey pairs (Z = –2.12, P = 0.034). In contrast, no significant difference was observed between white-white pairs and white-silver (median = 145.0, range = 136–160, n = 9; Z = 0.26, P = 0.80) or white-grey nest pairs (median = 147.0, range =

126–161, n = 12; Z = –0.403, P = 0.69). Similar to individual male color and hatching date, however, the results indicated a marginally non-significant difference in hatch date with white-silver pairs compared to silver-grey and grey-grey pairs combined (Z = –1.745, P = 0.081). No silver-silver nest pairs were observed in Kangerlussuaq.

Differences in hatch date and, more importantly, laying date relative to plumage color in Kangerlussuaq can provide clues as to why we observe predominately white individuals further north where breeding season duration is shorter. For example, selection in the form of crypsis or thermoregulation are two possible mechanisms that may influence plumage color distribution relative to reproductive success or lay date and temperature in Gyrfalcons; yet neither are mutually exclusive. Crypsis involves the ability to blend in with one's environment, thereby providing a higher likelihood to either escape predation or obtain prey, i.e., differential hunting success (see Bortolotti 2006 for a good review). Although there is no experimental evidence suggesting that hunting success depends on plumage color in Gyrfalcons, concealment may increase access to potential prey depending on the environment, e.g., white Gyrfalcons in snow cover or dark grey in forested habitat (but see Potopov and Sale 2005), particularly during the early breeding season when limited prey are available due to extreme cold temperatures.

Laying date may therefore reflect a males' ability to provide food to himself or his social mate (Skülason and Smith 1995), with white males being more competent to do so at earlier lay dates than grey males in Kangerlussuaq. For example, the distribution in laying date for each color variant in Kangerlussuaq may be the result of differential nest success with a larger number of nests associated with grey males failing before we are able to record nest site occupancy in the field. Similarly, we do not know whether females may preferentially choose white males over grey males early in the breeding season, i.e., sexual selection and mate choice (Roulin 2004), or whether white males arrive at the breeding site earlier than grey males, both of which could also explain these results. However, when expected frequencies of plumages of breeding pairs were generated, assuming random mating given the observed frequencies of plumages in both sexes for the entire breeding season, no evidence for assortative pairing based on plumage color in Kangerlussuaq was observed (Johnson and Burnham in review).

In a recent study in Kangerlussuaq, Booms and Fuller (2003a) documented variability in the amount of daily biomass delivered by the adult male at three different Gyrfalcon nests. Over one nesting season for example, one male delivered only 15% of the total prey items to the nest, with the female providing the majority of prey, whereas a second male at a different nest delivered 63% of all items. Interestingly, the former male was grey in plumage color, whereas the latter was white (T. Booms, pers. comm.). One must note, however, that this study did not record prey transfers away from the nest site. Primary prey early in the breeding season consisted of Rock Ptarmigan (*Lagopus muta*) and Arctic Hare leverets (*Lepus arcticus*), whereas passerines or sea birds, e.g., Dovekies (*Alle alle*) in Kangerlussuaq and Thule, respectively, made up a larger proportion of prey once those birds arrived later in the season, particularly for the smaller male Gyrfalcons compared to females (Booms and Fuller 2003a, b, Burnham 2008).

Likewise, plumage color differences may influence an individuals' metabolic cost associated with thermoregulation in the cold, which could also influence laying date by affecting the quality or condition of the male. The ability to reduce or increase heat load and maintain thermoneutrality has important implications for achieving an energy balance required for total daily energy expenditures among vertebrates, particularly during the breeding season when energy demands are

high. In birds, not only does plumage provide an insulating layer against cold weather, but its overall color (e.g., light vs. dark) also determines the proportions of incident solar radiation that are reflected or absorbed (Walsberg 1983, Wolf and Walsberg 2000). For example, white plumage can either increase or decrease individual heat gain depending on both structural properties and environmental conditions. Where normally dark plumage would provide maximum heat transfer to the skin or body because of its solar radiation absorbance properties, increased wind speeds can reduce solar radiation penetration toward the skin much more for dark plumages than white. In wind conditions above 6 m/sec, white plumage provides higher solar heat gain for birds compared to dark plumage when birds possess erected feathers or ptiloerection (Walsberg et al. 1978, Wolf and Walsberg 2000), a common behavior in birds to increase plumage insulation properties in cold weather. Therefore, there may be a selective advantage for white plumage in northern Greenland because the heat absorbed from solar radiation offsets the metabolic cost of thermoregulation in cold and windy (>6m/s) conditions. Ward et al. (2002) used similar arguments, but focused on reduced heat load to support dark plumage adaptation in desert environments.

For Gyrfalcons in Greenland, weather data, and specifically wind speed, suggest that conditions exist where white color variants may be at an advantage in their ability to thermoregulate more efficiently compared to grey or 'dark' individuals. Using weather data from the Danish Meteorological Institute (Carstensen and Jørgensen 2011) and Thule Air Base Weather Station recorded between 1981–2010, daily temperatures were similar when Gyrfalcons initiate egg laying in both Kangerlussuaq and Thule, despite approximately 18 days difference in mean lay date (date = 107.4, SD = 9.4, n = 70; date = 125.0, SD = 7.0, n = 40, respectively). Minimum and maximum lay dates include temperatures ranging from an average of –13.7˚C (SD = 8.7) on 28 March to 0.7˚C (SD = 0.9) on 9 May in Kangerlussuaq and –12.0˚C (SD = 4.5) on 24 April to –1.0˚C (SD = 2.7) on 24 May in Thule. Mean temperature for mean lay date in Kangerlussuaq and Thule were –5.8˚C (SD = 6.5) and –6.9˚C (SD = 3.4), respectively. Comparing different plumage colored males in Kangerlussuaq, the average daily temperature for mean Gyrfalcon lay date between 1981–2010 was approximately 3˚C colder for white males (mean = –5.8˚C, SD = 6.5) compared to grey (mean = –2.6˚ C, SD = 6.2; Z = –1.981, P = 0.048), and no difference in mean temperature was observed at lay date between nests with white and silver (mean = –6.2˚ C, SD = 7.0; Z = –0.126, P = 0.900) males. Mean temperature for mean nest lay date was colder for silver compared to grey males (Z = –2.159, P = 0.031).

Although wind speeds periodically exceeded 6 m/sec in Kangerlussuaq when Gyrfalcons are laying and incubating eggs, mean daily wind speed through April and May was 3.2 m/sec (SD = 1.3) and 3.8 m/sec (SD = 1.1), respectively. Mean daily wind speed when averaged over the past 30 years (1981–2010) never exceeded 4.5 m/sec for April and May. In Thule, mean daily wind speed for May and June was 8.7 (SD = 6.0) and 8.8 (SD = 5.9) m/sec, respectively. Mean daily wind speed when averaged over the past 30 years in Thule never dropped below 6.0 m/sec through May and June. In Kangerlussuaq, where wind speeds exceeded 6 m/sec much less frequently than Thule, other factors, such as increased physiological costs and energy expenditure associated with melanin production, including pleiotrophic effects, in dark Gyrfalcons during molt, may play a role in an individual's overall energy budget available for reproduction (Potapov and Sale 2005, see also Ducrest et al. 2008). Therefore, we are unable to reject the hypothesis that cold temperatures and wind speeds early in the breeding season may influence male reproductive success based on plumage color and a males' ability for ther-

moregulation or maintaining thermoneutrality (e.g., Wolf and Walsberg 2000).

White males in Kangerlussuaq are establishing a nest and therefore fledging young earlier in the breeding season compared to grey males (Figure 5), which is also the case with white-white breeding pairs as opposed to grey-grey pairs. In fact, a significant correlation between breeding pair plumage color and number of young documented at each nest was observed in Kangerlussuaq with dark pairs producing fewer offspring than light colored pairs (Spearman's Rho correlation r_s=0.383, n=42, P=0.012) after scaling the date of nest initiation relative to the day on which the first egg was laid for each year (Johnson and Burnham in review). In northern Greenland, therefore, the environment may restrict 'non-white' Gyrfalcon recruitment because a small window of opportunity exists for raising and fledging young (Drent 2006), and this window may be too small to maintain grey Gyrfalcons given potential limitations associated with obtaining prey and/or thermoregulation early in the breeding season across multiple generations. The range of dates that Gyrfalcons fledged from their nest in Kangerlussuaq included an additional 15 days compared to the range of dates observed in Thule (Burnham 2008). Therefore, directional selection for white plumage, including the influence of genetic drift and small population size, could create and maintain the conditions required to produce asymmetric dispersal patterns from north to south as was observed between Thule and Kangerlussauq in western Greenland (Johnson et al. 2007).

CONCLUSIONS

Population differentiation and various degrees of connectivity exist among Gyrfalcon populations, as reflected in the plumage color distributions (Johnson et al. 2007). Samples are required from Russia and Siberia to confirm whether one large population exists from north central Canada through Alaska to Norway. Similarly, additional samples from northeastern Canada, e.g., Ellesmere and Baffin Islands, will be important to investigate connectivity with Greenland as white Gyrfalcons have been observed in those areas. In Iceland, significant population differentiation exists compared to other sampled populations, suggesting isolation, which is further supported by limited plumage color, or lack of white and dark Gyrfalcons. Within Greenland and Ellesmere Island, where the most northern populations of Gyrfalcon exist, differing degrees of connectivity exist that are reflected in the distribution of plumage color variants. White plumage Gyrfalcons may be at an advantage compared to grey Gyrfalcons in Thule with only a single grey female observed during a single breeding season over the past 17 years. Both crypsis and thermoregulation through selection may be important factors influencing plumage color distributions by influencing the 'quality' of the breeding male allowing for earlier lay date and sufficient time for offspring development prior to autumn migration.

Despite Icelandic Gyrfalcons possessing the 'white' MC1R allele in relatively high frequency (10/22 individuals), no Gyrfalcons sampled during the breeding season were observed as homozygous for this allele and no breeders with white phenotypes have been observed to date despite ringing over 1500 chicks (O. Nielsen, pers. comm.). Some form of selection may be negatively influencing 'white' Gyrfalcon survival in Iceland. The precise mechanism is not known and certainly deserves further study. It is interesting to note, however, that Iceland Gyrfalcon nests are more accessible to humans (and presumably to potential nest predators, e.g., Arctic Fox, *Vulpes lagopus*), than elsewhere in their circumpolar distribution where access to nests often requires climbing equipment and protection (pers. observ.). Possible factors worth exploring, that may influence plumage color distribution in Iceland, include those associated with predation pressure at Gyrfalcon nest sites. Alternatively, extensive land use change

and deforestation in Iceland has occurred over the recent past (McGovern et al. 2007, Vickers et al. 2011), and the current Gyrfalcon plumage color distribution may reflect more historic processes.

Alternatively, given the significant population genetic differentiation observed with the Iceland Gyrfalcon population relative to other sampled locations, multiple genes or a different gene entirely may influence plumage color pigment production similar to what has been reported in other intraspecific studies (Steiner et al. 2007, Pointer and Mundy 2008, Hubbard et al. 2010). More work is required to identify whether additional genes or regulatory mechanisms (e.g., transcription factors, cis-regulatory elements) exist with Gyrfalcons that may contribute to plumage color and banding pattern differences among variants (see McKinnon and Pierotti 2010). Further, statistical associations between MC1R mutations and color patterns should be functionally verified similar to work done with mammals (Steiner et al. 2009) and reptiles (Rosenblum et al. 2010). The nonsynonymous mutations observed in MC1R in Gyrfalcons (Johnson et al. 2012) may have no measurable effect on receptor function in regulating melanin production, and covariation in plumage color and other traits may in fact be due to linkage with genes that influence egg-lay-date and/or factors related to timing of reproduction or possibly pleiotrophic effects (Hubbard et al. 2010, McKinnon and Pierotti 2010) such as those associated with immune response (Gangoso et al. 2011).

As climate continues to change and both wintering and breeding distributions shift or fail to shift to accommodate to temperatures (Saino et al. 2011), we are likely to observe a changing distribution or mixture of Gyrfalcon plumage color variants in northern Greenland before local extinction (e.g., Maloney et al. 2009, Gratten et al. 2010, Maloney et al. 2010), provided that other factors do not eliminate the species first, e.g, competition with Peregrine Falcons, *Falco peregrinus,* for nest site and food resources (Burnham 2008). Knowing the evolutionary processes that have led to and maintained the current Gyrfalcon distribution is of use for predicting how the species may respond to challenges it may face in the future.

Acknowledgments

We thank the organizers of this conference and the many, many individuals and organizations that made this work possible. We would particularly like to thank B. and R. Mutch, J. Cafferty, J. Stephens, B. Heinrich, B. Konkel, C. Sandfort, J. Willmarth, E. Gott, and R. Haswell for assistance in collecting samples in Greenland. We thank Ó. Nielsen and the Ministry for the Environment for assistance in Iceland, C. Cyrus for help obtaining samples from Alaska, and M. Nesje and J. Lifjeld for microsatellite data from Norway. We also thank the falconers in Alaska who generously provided tissue samples from their own wild-taken birds. J. Stevens provided the weather data for Thule study area. Work in Greenland is in cooperation with and authorized by the Commission for Scientific Research in Greenland, Greenland Home Rule Government, the Danish Polar Center, and the US Air Force. In Alaska, our activities were authorized by the Alaska Department of Fish and Game with special assistance from K. Titus and W. Regelin. We thank the residents of Thule Air Base, the 109th Air National Guard, National Science Foundation, VECO Polar Associates and R. Abbott, E. Stockard, T. Quinn, E. Vaughn, and S. Zager. Additional thanks to B. Brodersen, B. Vængtoft, and K. Bahr Friis of KISS. Financial support was provided by University of North Texas, The Peregrine Fund, R. Mutch, P. Pfendler, R. Wasendorf, J. Stephens, Gordon and Betty Moore Foundation, The Charles Engelhard Foundation, The Wolf Creek Charitable Foundation, The Offield Family Foundation, and Bennu and the Florence Hegyi Family Trust.

LITERATURE CITED

ABBOTT, R. J., AND C. BROCHMANN. 2003. History and evolution of the arctic flora: In the footsteps of Eric Hultén. Molecular Ecology 12:299–313.

ÆGISDÓTTIR, H. H., AND Þ. E. ÞÓRHALLSDÓTTIR. 2004. Theories on migration and history of the North-Atlantic flora: A review. Jökull 54:1–16.

ANDERSEN, B. G., AND H. W. BORNS, JR. 1994. The Ice Age World: An Introduction to Quaternary History and Research with Emphasis on North America and Europe During the Last 2.5 Million Years. Scandinavian University Press, Oslo, Norway.

ANDERSON, T. M., B. M. VONHOLDT, S. I. CANDILLE, M. MUSIANI, C. GRECO, D. R. STAHLER, D. W. SMITH, B. PADHUKASAHASRAM, E. RANDI, J. A. LEONARD, C. D. BUSTAMANTE, E. A. OSTRANDER, H. TANG, R. K. WAYNE, AND G. S. BARSH. 2009. Molecular and evolutionary history of melanism in North American Gray Wolves. Science 323:1339–1343.

BAIÃO, P. C., E. A. SCHREIBER, AND P. G. PARKER. 2007. The genetic basis of the plumage polymorphism in Red-footed Boobies (*Sula sula*): A melanocortin-1 receptor (MC1R) analysis. Journal of Heredity 98:287–292.

BENNETT, D. C., AND M. L. LAMOREUX. 2003. The color loci of mice—a genetic century. Pigment Cell Research 16:333–344.

BENNIKE, O. 1999. Colonisation of Greenland by plants and animals after the last ice age: A review. Polar Record 35:323–336.

BOOMS, T. L., AND M. R. FULLER. 2003a. Gyrfalcon feeding behavior during the nestling period in central west Greenland. Arctic 56:341–348.

BOOMS, T. L., AND M. R. FULLER. 2003b. Gyrfalcon diet in central west Greenland during the nesting period. Condor 105:528–537.

BORTOLOTTI, G. R. 2006. Natural selection and coloration: Protection, concealment, advertisement, or deception? Pages 3–35 *in* G. E. Hill and K. J. McGraw (Eds.). Bird Coloration, vol. 2. Function and Evolution. Harvard University Press, Cambridge, Massachusetts, USA.

BORTOLOTTI, G. R., L. M. GONZÁLEZ, A. MARGALIDA, R. SÁNCHEZ, AND J. ORIA. 2008. Positive assortative pairing by plumage color in Spanish Imperial Eagles. Behavioural Processes 78:100–107.

BROOKE, M. DE L. 2010. Unexplained recurrent features of plumage of birds. Ibis 152:845–847.

BRUNHOFF, C., K. E. GALBREATH, V. B. FEDOROV, J. A. COOK, AND M. JAAROLA. 2003. Holarctic phylogeography of the Root Vole (*Microtus oeconomus*): Implications for late Quaternary biogeography of high latitudes. Molecular Ecology 12:957–968.

BUCKLAND, P., AND A. DUGMORE. 1991. 'If this is a refugium, why are my feet so bloody cold?' The origins of the Icelandic biota in the light of recent research. Pages 107–125 *in* J. K. Maizels and C. Caseldine (Eds.). Environmental Change in Iceland: Past and Present. Kluwer Academic Publishers, Netherlands.

BURNHAM, K. K. 2008. Inter- and intraspecific variation of breeding biology, movements, and genotype in Peregrine Falcon *Falco peregrinus* and Gyrfalcon *F. rusticolus* populations in Greenland. D. Phil. Thesis, University of Oxford, Oxford, UK.

BURNHAM, K. K., AND I. NEWTON. 2011. Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea. Ibis 153:468–484.

CADE, T. J. 1982. Falcons of the World. Williams Collins Sons & Co. Limited, London, UK.

CADE, T. J., P. KOSKIMIES, AND Ó. NIELSEN. 1998. *Falco rusticolus* Gyrfalcon. Pages 1–25 *in* S. Cramp (Ed.). Birds of the Western Palearctic Update, vol. 2, no. 1. Oxford University Press, UK.

CARSTENSEN, L. S., AND B. V. JØRGENSEN. 2011. Weather and Climate Data from Greenland 1958–2010. Technical Report

11–10. Danish Meteorological Institute, Copenhagen, Denmark.

Chang, V. S., J. Lejeune, and K. M. Cheng. 2010. The pattern of inheritance of melanin-based plumage color variants in the Gyrfalcon (*Falco rusticolus*). Journal of Raptor Research 44:224–232.

Cheviron, Z. A., S. J. Hackett, and R. T. Brumfield. 2006. Sequence variation in the coding region of the melanocortin-1 receptor gene (MC1R) is not associated with plumage variation in the Blue-crowned Manakin (*Lepidothrix coronata*). Proceedings of the Royal Society B 273:1613–1618.

Dahl, E. 1955. Biogeographic and geological indications of unglaciated areas in Scandinavia during the glacial ages. Bulletin of the Geological Society of America 66:1499–1519.

Drent, R. H. 2006. The timing of birds' breeding seasons: The Perrins hypothesis revisited especially for migrants. Ardea 94:305–322.

Driskell, A. C., R. O. Prum, and S. Pruett-Jones. 2010. The evolution of black plumage from blue in Australian fairy-wrens (Maluridae): Genetic and structural evidence. Journal of Avian Biology 41:505–514.

Ducrest, A. –L., L. Keller, and A. Roulin. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. Trends in Ecology & Evolution 23:502–510.

Eldredge, N. 2001. The sixth extinction. Action Bioscience June. http://www.actionbioscience.org/newfrontiers/eldredge2.html

Ellis, D. H., C. H. Ellis, G. W. Pendleton, A. V. Panteleyev, I. V. Rebrova, and Y. M. Markin. 1992. Distribution and color variation of Gyrfalcons in Russia. Journal of Raptor Research 26:81–88.

Fedorov, V. B., and N. C. Stenseth. 2002. Multiple glacial refugia in the North American Arctic: Inference from phylogeography of the Collared Lemming (Dicrostonyx groenlandicus). Proceedings of the Royal Society Series B 269:2071–2077.

Flann, I. 2003. Gyrfalcon color variation. Journal of Raptor Research 37:173–174.

Fuller, M., D. Holt, and L. Schueck. 2003. Snowy Owl movements: Variation on the migration theme. Pages 359–366 *in* P. Berthold P., E. Gwinner, and E. Sonnenschein, (Eds.). Avian Migration. Springer-Verlag, Berlin, Heidelberg, Germany.

Gangoso, L., J. M. Grande, A. –L. Ducrest, J. Figuerola, G. R. Bortolotti, J. A. Andrés, and A. Roulin. 2011. MC1R-dependent, melanin-based colour polymorphism is associated with cell-mediated response in the Eleonora's Falcon. Journal of Evolutionary Biology (in press).

García-Barron, J. C., B. L. Sánchez-Laorden, and C. Jiménez-Cervantes. 2005. Melanocortin-1 receptor structure and functional regulation. Pigment Cell Research 18:393–410.

Gasparini, J., R. Piault, P. Bize, and A. Roulin. 2009. Synergistic and antagonistic interaction between different branches of the immune system is related to melanin-based coloration in nestling Tawny Owls. Journal of Evolutionary Biology 22:2348–2353.

Gluckman, T.-L., and G. C. Cardoso. 2010. The dual function of barred plumage in birds: Camouflage and communication. Journal of Evolutionary Biology 23:2501–2506.

Gratten, J., A. J. Wilson, A. F. McRae, D. Beraldi, P. M. Visscher, J. M. Pemberton, and J. Slate. 2010. No evidence for warming climate theory of coat colour change in Soay sheep: A comment on Maloney et al. Biology Letters 6:678–679.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society 58:247–276.

Hewitt, G. M. 2004. The structure of biodiversity-insights from molecular phylogeography. Frontiers in Zoology 1:4.

HOEKSTRA, H. E. 2006. Genetics, development and evolution of adaptive pigmentation in vertebrates. Heredity 97:222–234.

HOEKSTRA, H. E., R. J. HIRSCHMANN, R. A. BUNDEY, P. A. INSEL, AND J. P. CROSSLAND. 2007. A single amino acid mutation contributes to adaptive Beach Mouse color pattern. Science 313:101–104.

HOFFMANN, A. A., AND C. M. SGRÒ. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

HOLDER, K., R. MONTGOMERIE, AND V. L. FRIESEN. 1999. A test of the glacial refugium hypothesis using patterns of mitochondrial and nuclear DNA sequence variation in Rock Ptarmigan (*Lagopus mutus*). Evolution 53:1936–1950.

HUBBARD, J. K., J. A. UY, M. E. HAUBER, H. E. HOEKSTRA, AND R. J. SAFRAN. 2010. Vertebrate pigmentation: From underlying genes to adaptive function. Trends in Genetics 26:231–239.

HUGHES, J. B., G. C. DAILY, P. R. EHRLICH. 1997. Population diversity: Its extent and extinction. Science 278:689–692.

HULL, J. M., D. P. MINDELL, S. L. TALBOT, E. H. KAY, H. E. HOEKSTRA, AND H. B. ERNEST. 2010. Population structure and plumage polymorphism: The intraspecific evolutionary relationships of a polymorphic raptor, *Buteo jamaicensis harlani*. BMC Evolutionary Biology 10: 224.

IPCC. 2007. Summary for policymakers. Pages 1–18 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, and M. Marquis (Eds.). Climate change 2007: The Physical Science Basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK.

JACQUIN, L., P. LENOUVEL, C. HAUSSY, S. DUCATEZ, AND J. GASPARINI. 2011. Melanin-based coloration is related to parasite intensity and cellular immune response in an urban free living bird: The feral pigeon *Columba livia*. Journal of Avian Biology 42:11–15.

JOHNSEN, P. 1953. Birds and mammals of Peary Land in North Greenland. Meddelelser om Grønland 128:1–138.

JOHNSON, J. A., A. D. AMBERS, AND K. K. BURNHAM. 2012. Genetics of plumage color in the Gyrfalcon (*Falco rusticolus*): Analysis of the melanocortin-1 receptor gene. Journal of Heredity (in press).

JOHNSON, J. A., AND K. K. BURNHAM. (in review) Timing of breeding influences plumage color distribution in the arctic Gyrfalcon.

JOHNSON, J. A., K. K. BURNHAM, W. A. BURNHAM, AND D. P. MINDELL. 2007. Genetic structure among continental and island populations of Gyrfalcons. Molecular Ecology 16:3145–3160.

KAUFMAN, D. S., D. P. SCHNEIDER, N. P. MCKAY, C. M. AMMANN, R. S. BRADLEY, K. R. BRIFFA, G. H. MILLER, B. L. OTTO-BLIESNER, J. T. OVERPECK, B. M. VINTHER, AND ARCTIC LAKES 2K PROJECT MEMBERS. 2009. Recent warming reverses long-term arctic cooling. Science 325:1236–1239.

KERJE, S., J. LIND, K. SCHUTZ, P. JENSEN, AND L. ANDERSSON. 2003. Melanocortin-1 receptor (MC1R) mutations are associated with plumage colour in chicken. Animal Genetics 34:241–248.

KOCH, L. 1925. Nord om Grønland. Køvenhavn, Denmark.

LING, M. K., M. C. LAGERSTROM, R. FREDRIKSSON, R. OKIMOTO, N. I. MUNDY, S. TAKEUCHI, AND H. B. SCHIÖTH. 2003. Association of feather colour with constitutively active melanocortin 1 receptors in chicken. European Journal of Biochemistry 270:1441–1449.

MALONEY, S. K., A. FULLER, AND D. MITCHELL. 2009. Climate change: Is the dark Soay sheep endangered? Biology Letters 5:826–829.

MALONEY, S. K., A. FULLER, AND D. MITCHELL. 2011. A warming climate remains a plausible hypothesis for the decrease in dark Soay sheep: An invited reply. Biology Letters 6:680–681.

Marthinsen, G., L. Wennerberg, R. Solheim, and J. T. Lifjeld. 2009. No phylogeographic structure in the circumpolar Snowy Owl (*Bubo scandiacus*). Conservation Genetics 10:923–933.

McGovern, T. H., O. Vésteinson, A. Fridriksson, M. Church, I. Lawson, I. A. Simpson, A. Einarsson, A. J. Dugmore, G. T. Cook, S. Perdikaris, K. J. Edwards, A. M. Thomson, W. P. Adderley, A. J. Newton, G. Lucas, R. Edvardsson, O. Aldred, and E. Dunbar. 2007. Landscapes of settlement in northern Iceland: Historical ecology of human impact and climate fluctuation on the millennial scale. American Anthropologist 109:27–51.

McGraw, K. J. 2006. Mechanics of melanin-based coloration. Pages 243–294 *in* G. E. Hill and K. J. McGraw (Eds.). Bird Coloration, vol. 1. Mechanisms and Measurments. Harvard University Press, Cambridge, Massachusetts, USA.

McIntyre, C. L., D. C. Douglas, and L. G. Adams. 2009. Movements of juvenile Gyrfalcons from western and interior Alaska following departure from their natal areas. Journal of Raptor Research 43:99–109.

McKinnon, J. S., and M. E. R. Pierotti. 2010. Colour polymorphism and correlated characters: Genetic mechanisms and evolution. Molecular Evolution 19:5101–5125.

Mullen, L. M., S. N. Vignieri, J. A. Gore, and H. E. Hoekstra. 2009. Adaptive basis of geographic variation: Genetic, phenotypic and environmental differences among Beach Mouse populations. Proceedings of the Royal Society Series B 276:3809–3818.

Mundy, N. I. 2005. A window on the genetics of evolution: MC1R and plumage colouration in birds. Proceedings of the Royal Society Series B 272:1633–1640.

Mundy, N. I. 2006. Genetic basis of color variation in wild birds. Pages 469–506 *in* G. E. Hill and K. J. McGraw (Eds.). Bird Coloration, vol. 1. Mechanisms and Measurements. Harvard University Press, Cambridge, Massachusetts.

Mundy, N. I., N. S. Badcock, T. Hart, K. Scribner, K. Janssen, and N. J. Nadeau. 2004. Conserved genetic basis of a quantitative plumage trait involved in mate choice. Science 303:1870–1873.

Nadeau, N. J., F. Minvielle, and N. I. Mundy. 2006. Association of a Glu92Lys substitution in MC1R with extended brown in Japanese Quail (*Coturnix japonica*). Animal Genetics 37:287–289.

Newton, I. 2003. Speciation and Biogeography of Birds. Academic Press, London, UK.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37:637–669.

Pielou, E. C. 1991. After the Ice Age: The Return of Life to Glaciated North America. The University of Chicago Press, Chicago, Illinois, USA.

Ploeger, P. L. 1968. Geographical differentiation in arctic Anatidae as a result of isolation during the last glacial. Ardea 56:1–155.

Pointer, M. A., and N. I. Mundy. 2008. Testing whether macroevolution follows microevolution: Are colour differences among swans (*Cygnus*) attributable to variation at the MC1R locus? BMC Evolutionary Biology 8:249.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Høye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358.

Potapov, E., and R. Sale. 2005. The Gyrfalcon. Yale University Press, New Haven, Connecticut, USA.

PROVAN, J., AND K. D. BENNETT. 2008. Phylogeographic insights into cryptic glacial refugia. Trends in Ecology and Evolution 23:564–571.

RASMUSSEN, N., F. NELSON, P. GOVITRAPONG, AND M. EBADI. 1999. The actions of melanin and melanocyte stimulating hormone (MSH). Neuroendocrinology Letters 20:265–282.

ROSENBLUM, E. B., H. RÖMPLER, T. SCHÖNEBERG, AND H. E. HOEKSTRA. 2010. Molecular and functional basis of phenotypic convergence in white lizards at White Sands. Proceedings of the National Academy of Sciences USA 107:2113–2117.

ROULIN, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphisms in birds. Biological Reviews 79:815–848.

SAINO, N., R. AMBROSINI, D. RUBOLINI, J. VON HARDENBERG, A. PROVENZALE, K. HÜPPOP, O. HÜPPOP, A. LEHIKOINEN, E. LEHIKOINEN, K. RAINIO, M. ROMANO, AND L. SOKOLOV. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society Series B 278:835–842.

SALOMONSEN, F. 1972. Zoological and ecological problems in arctic birds. Pages 25–77 *in* K. H. Voous (Ed.). Proceedings of the XVth International Ornithological Congress. E. J. Brill, Netherlands.

SKOGLUND, P., AND J. HÖGLUND. 2010. Sequence polymorphism in candidate genes for differences in winter plumage between Scottish and Scandinavian Willow Grouse (*Lagopus lagopus*). PLoS ONE 5:e10334.

SKÜLASON, S., AND T. B. SMITH. 1995. Resource polymorphisms in vertebrates. Trends in Ecology and Evolution 10:366–370.

SNOW, C. 1974. Gyrfalcon, *Falco rusticolus*. Habitat management series for unique or endangered species, Report No. 9, Technical Note T-N-241. US Department of Interior, Bureau of Land Management. Denver, Colorado, USA.

STEINER, C. C., H. RÖMPLER, L. M. BOETTGER, T. SCHÖNEBERG, AND H. E. HOEKSTRA. 2009. The genetic basis of phenotypic convergence in Beach Mice: Similar pigment patterns but different genes. Molecular Biology and Evolution 26:35–45.

STEINER, C. C., J. N. WEBER, AND H. E. HOEKSTRA. 2007. Adaptive variation in Beach Mice produced by two interacting pigmentation genes. PLoS Biology 5(9): e219

STEWART, J. R., AND A. M. LISTER. 2001. Cryptic northern refugia and the origins of the modern biota. Trends in Ecology and Evolution 16:608–613.

STEWART, J. R., A. M. LISTER, I. BARNES, AND L. DALÉN. 2010. Refugia revisited: Individualistic responses of species in space and time. Proceedings of the Royal Society Series B 277:661–671.

TAKEUCHI, S., S. TAKAHASHI, S. OKIMOTO, H. B. SCHIOTH, AND T. BOSWELL. 2003. Avian melanocortin system: Alpha-MSH may act as an autocrine/paracrin hormone—a mini review. Annals of the New York Academy of Sciences 994:366–372.

THERON, E., K. HAWKINS, E. BERMINGHAM, R. E. RICKLEFS, AND N. I. MUNDY. 2001. The molecular basis of an avian plumage polymorphism in the wild: A melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the Bananaquit, *Coereba flaveola*. Current Biology 11:550–557.

TICKELL, W. L. N. 2003. White plumage. Waterbirds 26:1–12.

TODD, W. E. C., AND H. FRIEDMANN. 1947. A study of the Gyrfalcons with particular reference to North America. The Wilson Bulletin 59:139–150.

UY, J. A. C., R. G. MOYLE, C. E. FILARDI, AND Z. A. CHEVIRON. 2009. Difference in plumage color used in species recognition between incipient species is linked to a single amino acid substitution in the melanocortin-1 receptor. American Naturalist 174:244–254.

VAURIE, C. 1961. Systematic notes on palearctic birds, no. 45, Falconidae: The genus

Falco (part 2). American Museum Novitates 2038:1–24.

VICKERS, K., E. ERLENDSSON, M. J. CHURCH, K. J. EDWARDS, AND J. BENDING. 2011. 1000 years of environmental impact at Stóra-Mörk, southern Iceland: A multiproxy study of a dynamic and vulnerable landscape. Holocene (in press). http://dx.doi.org/10.1177/0959683611400201

VISSER, M. E. 2008. Keeping up with a warming world: Assessing the rate of adaptation to climate change. Proceedings of the Royal Society Series B 275:649–659.

VITOUSEK, P. M., H. A. MOONEY, J. LUBCHENCO, AND J. M. MELILLO. 1997. Human domination of Earth's ecosystems. Science 277:494–499.

WALSBERG, G. E. 1983. Coat color and solar heat gain in animals. BioScience 33:88–91.

WALSBERG, G. E., G. S. CAMPBELL, AND J. R. KING. 1978. Animal coat color and radiative heat gain: A re-evaluation. Journal of Comparative Physiology B 126:211–222.

WALTARI, E., AND J. A. COOK. 2005. Hares on ice: phylogeography and historical demographics of *Lepus arcticus, L. othus,* and *L. timidus* (Mammalia: Lagomorpha). Molecular Ecology 14:2005–3016.

WALTARI, E., J. R. DEMBOSKI, D. R. KLEIN, AND J. A. COOK. 2004. A molecular perspective on the historical biogeography of the northern high latitudes. Journal of Mammalogy 85:591–600.

WARD, J. M., J. D. BLOUNT, G. D. RUXTON, AND D. C. HOUSTON. 2002. The adaptive significance of dark plumage for birds in desert environments. Ardea 90:311–323.

WHITE, C. M., AND T. J. CADE. 1971. Cliff-nesting raptors and ravens along the Colville River in arctic Alaska. The Living Bird 10:107–150.

WINKER, K. 2009. Reuniting phenotype and genotype in biodiversity research. BioScience 59:657–665.

WOLF, B. O., AND G. E. WALSBERG. 2000. The role of the plumage in heat transfer processes in birds. American Zoologist 40:575–584.