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The Genetic Basis of the Plumage Polymorphism in Red-Footed Boobies (*Sula sula*): a *Melanocortin-1 Receptor* (*MC1R*) Analysis

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Abstract

The red-footed booby (*Sula sula*) is considered one of the most polymorphic seabirds, with 3 recognized major adult plumage types: 1) white, 2) white-tailed brown, and 3) brown and several degrees of intermediates. Here we show that the white/melanic polymorphism observed in this species is perfectly associated with 2 point substitutions, *Val85Met* and *His207Arg*, at the *melanocortin-1 receptor* (*MC1R*) gene. Among the melanic plumage variants, we also found a strong association between the degree of melanism and the number of copies of variant *MC1R* alleles. Furthermore, the *Val85Met* point substitution has been previously shown to be associated with melanic phenotypes in the lesser snow goose (*Anser c. caerulescens*), suggesting parallel evolution of the melanic allele, and hence, melanism, between these 2 distantly related species. We also compared the *MC1R* locus in red-footed boobies with a nonpolymorphic congener, the Nazca booby (*Sula granti*), in which all adults are white. We found that Nazca boobies present the same genotype at sites 85 and 207 as white morph red-footed boobies.

Plumage color variation in birds has long attracted the attention of ecologists and evolutionary biologists, and it has been studied in various contexts, such as sexual selection, sexual dimorphism, speciation, and the establishment and maintenance of polymorphisms (Mundy 2005). It is broadly recognized that plumage color variation has a strong genetic component. However, until recently, there has been little progress in understanding the genetic mechanisms underlying different color morphs in wild populations.

Melanic plumage polymorphism is found in a variety of bird families, and among seabirds, it has arisen independently in 4 families: Procellariidae, Hydrobatidae, Stercorariidae, and Sulidae (Le Corre 1999). In the Sulidae family, comprising 9 species of gannets and boobies, the red-footed booby (*Sula sula*) is 1 of 2 polymorphic species along with the brown booby (*Sula leucogaster*) (Nelson 1978), and it is considered one of the most polymorphic seabirds (Le Corre 1999). Plumage patterns in seabirds are not usually very variable (Pierotti 1987), and therefore, the striking plumage variation found in red-footed boobies is rare among seabirds.

In red-footed boobies, there are 3 major adult plumage types and several degrees of intermediates. The main color morphs recognized by Nelson (1978) are the white, the white-tailed brown, and the brown (see also color morphs described in Schreiber et al. 1996). In the Galápagos archipelago, 2 color morphs are recognized: 1) brown and 2) white and various degrees of intermediates. The intermediate plumage is characterized by almost complete brown plumage with various numbers of white feathers in the scapular region. In this archipelago, there is quantitative variation in the degree of melanism between the brown morph and the intermediate, and discrete separation between these and the white morph. On Johnston Atoll, all 5 color morphs described by Schreiber et al. (1996) are found, and there is continuous variation between the morphs with the intermediate morphs characterized by mostly brown plumage with various degrees of white throughout the body. The white morph is the most common along the species' range and the brown morph is the rarest, known to occur commonly in only 2 places: the Galápagos archipelago and Cocos Island, both in the eastern Pacific (Nelson 1978).

In the Galápagos archipelago, red-footed boobies are found on 4 islands: Darwin, Wolf, San Cristóbal, and Genovesa. Genovesa holds one of the largest colonies of

red-footed boobies in the world, with a population estimated around 140 000 pairs (Nelson 1978). In the Genovesa, San Cristóbal, and Wolf populations, approximately 10% of the birds are of the white morph, and brown and intermediate morphs account for the remaining 90% (Baião PC and Parker PG, unpublished data); this is opposite the proportions found across the world's populations in this pantropical species (~90% white, 10% brown). The Darwin population has a slightly different proportion of color morphs, with white birds representing approximately 30% of the birds and brown and intermediate birds accounting for the remaining 70% (Baião PC and Parker PG, unpublished data) (Figure 1). Also, on all the islands of this archipelago, the white morph has a blackish tail, which does not occur commonly elsewhere (Nelson 1968), although it has been recorded on Johnston Atoll. On Johnston Atoll, the white morph comprises 78% of the population (Schreiber et al. 1996).

The Nazca booby (*Sula granti*) was recently elevated from a masked booby subspecies (*Sula dactylatra granti*) to a full species status (Friesen et al. 2002). The new classification was proposed based on morphological and behavioral differences (Pitman and Jehl 1998) and it was later supported by molecular data on mitochondrial cytochrome *b* (Friesen et al. 2002). Unlike the red-footed boobies, Nazca boobies are not polymorphic, and both males and females present bright white plumage, except for the black distal half of the secondaries, tertiaries, and rectrices (Pitman and Jehl 1998). Thus, their plumage pattern is very close to that of white morph red-footed boobies.

The *Melanocortin-1-receptor* gene (*MC1R*) encodes the MC1R protein, which is expressed in the melanocytes of developing feathers and hair and plays a critical role in the control of melanin synthesis (Theron et al. 2001). The MC1R protein is a 7-transmembrane domain G-protein–coupled receptor (Mountjoy et al. 1992), which is activated by melanocyte-stimulating hormone (MSH), leading to an increase in black/brown eumelanin production that is transferred to the surrounding feathers. Low activity generally leads to the default pathway stimulating the production of yellow/red pheomelanin (García-Borrón et al. 2005). The *MC1R* gene has a coding region of around 945 bp, with variation among taxonomic groups. Associations between point mutations at this locus and polymorphisms based on melanin have been shown for a variety of taxa, such as fish (Logan et al. 2003), reptiles (Rosenblum et al. 2004), birds (Doucet et al. 2004; Mundy et al. 2004; Takeushi et al. 1996; Theron et al. 2001), and mammals (Eizirik et al. 2003; Hoekstra et al. 2004; Mundy and Kelly 2003; Nachman et al. 2003; Robbins et al. 1993). In all 3 wild bird species for which the *MC1R* locus has been analyzed (*Coereba flaveola*, *Stercorarius parasiticus*, and *Anser c. caerulescens*) (Mundy et al. 2004; Theron et al. 2001), single point substitutions were shown to be related to dramatic melanism differences.

In this study, we explore the relationship between plumage polymorphism in red-footed boobies and allelic variation at the *MC1R* gene. Based on previous studies that analyzed the *MC1R* locus and plumage variation in wild birds, we predict that point substitutions at the *MC1R* locus may explain the plumage variation observed in this species. We also compared the *MC1R* locus of red-footed boobies with a nonpolymorphic congener, the Nazca booby. Because this species shows a plumage pattern similar to that of white morph red-footed boobies, we predict no difference at the *MC1R* locus between Nazca boobies and white morph red-footed boobies.

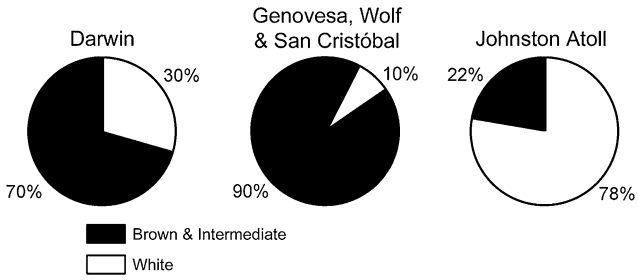

Figure 1. Proportion of color morphs in 5 different locations. Black represents brown and intermediate morphs and white represents the white morph.

Methods

This study was conducted on 2 archipelagos in the Pacific Ocean, the Galápagos archipelago and Johnston Atoll. The Galápagos archipelago is located about 1000-km west of the mainland of Ecuador. It is a volcanic archipelago that has never been connected to the mainland, and 97% of its area has been maintained as a National Park since 1959. Johnston Atoll is a National Wildlife Refuge of the U.S. Fish and Wildlife Service, located approximately 1328-km southwest of Honolulu, also never connected to any mainland. The atoll consists of 4 islands and it was a U.S. military base previously, but it has been uninhabited since 2003. Red-footed boobies nest in colonies on both archipelagos.

One hundred and twelve adult red-footed boobies with fully developed plumage coloration were sampled, and all individuals were classified into 3 categories: 1) brown, 2) white, and 3) intermediate. Intermediate morphs in the Galápagos archipelago consisted of individuals with brown plumage and various numbers of white feathers in the scapular region; on Johnston Atoll, intermediates consisted of brown individuals with various numbers of white feathers throughout the body. The samples were collected from 4 geographic locations, 3 in the Galápagos archipelago: Genovesa (45 birds: 22 white, 16 brown, and 7 intermediate), Darwin (18 birds: 4 white, 5 brown, and 9 intermediate), and Wolf (29 birds: 10 white, 10 brown, and 9 intermediate), and on Johnston Atoll (20 birds: 11 white, 6 brown, and 3 intermediate). In addition, 5 Nazca boobies were sampled from Isla Genovesa in Galápagos for comparison. In all cases, birds were captured by hand and 50 μl of blood was collected via the brachial vein and preserved in lysis buffer (Longmire et al. 1988).

Genomic DNA was extracted using standard phenol/chloroform extraction protocol. After extraction, a 650-bp

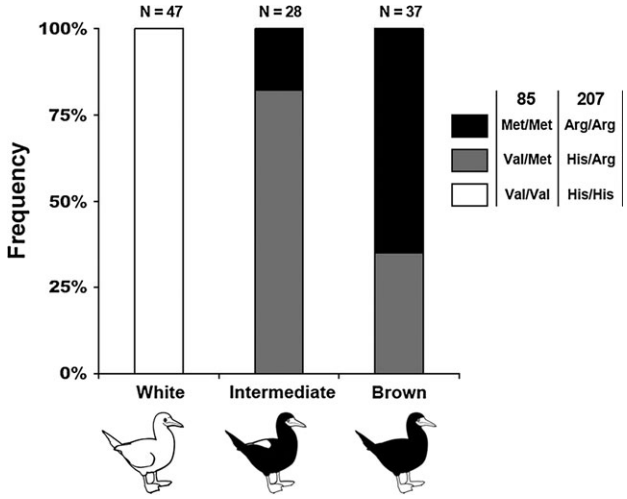

Figure 2. Frequency of genotypes at sites 85 and 207 per color morph. *N* represents the number of individuals sampled in each color morph category.

fragment of the 945-bp avian *MC1R*-coding region was amplified via polymerase chain reaction (PCR) using primers *MSHR72* (5′-ATGCCAGTGAGGGCAACCA-3′) and *MSHR9* (5′-CTGGCTCCGGAAGGCATAGAT-3′) (Mundy et al. 2004). PCR amplifications were performed with the following cycling parameters: 94 °C for 2 min, 35× (94 °C for 30 s, 63–66 °C for 45 s, 72 °C for 90 s), and 72 °C for 5 min. The PCR products were directly sequenced on both strands, using standard cycle sequencing protocols. Sequences were edited in Seqman II (version 6.1).

Sequences were aligned by eye in MacClade 4.06 (Maddison DR and Maddison WP 2003). Assignment of associations of variable sites and color morphs was obtained through visual interpretation of unambiguously aligned sequences. Statistical support for *MC1R* phenotype–genotype associations was performed using a 2 × 2 contingency table and Fisher's exact test.

Results

A fragment of the coding region (650 bp) of the *MC1R* gene was sequenced for a total of 47 white, 28 intermediate, and 37 brown individuals of red-footed boobies and 5 individuals of Nazca boobies. A total of 4 nonsynonymous variable sites were found on the 650-bp–sequenced fragment among red-footed boobies. Two nonsynonymous point substitutions (*Val85Met* and *His207Arg*) in the *MC1R* gene were found to be perfectly associated with color variation in all 4 geographic locations sampled (Figure 2). The 2 sites were in complete linkage disequilibrium, and only 3 of the 9 possible combinations were found among all sequenced birds. If an individual was homozygous at site 85 for valine, it was also homozygous at site 207 for histidine. If it was heterozygous at site 85, it was also heterozygous at site 207. And finally, if it was homozygous at site 85 for methionine, it was also homozygous at site 207 for arginine (Table 1).

All the white morph red-footed boobies sampled (N = 47) were homozygous for the Val^{85} and the His^{207} alleles, whereas all the melanic birds (brown, white-tailed brown, and intermediates) sampled (N = 84) were homozygous or heterozygous for the Met^{85} and Arg^{207} alleles (Fisher's exact test, $P < 0.001$). Furthermore, the degree of melanism depended on the number of Met^{85} and Arg^{207} alleles (2 × 2 contingency table, $\chi^2 = 12.41$; $P < 0.001$), meaning that birds categorized as brown were more likely to be homozygous for Met^{85} and Arg^{207}, whereas birds categorized as intermediates were more likely to be heterozygous at sites 85 and 207 (Figure 2). All 5 Nazca boobies sequenced were homozygous for Val^{85} and His^{207}, and 6 nonsynonymous substitutions were found between white morph red-footed boobies and Nazca boobies: *Val55Met*, *Val80Ileu*, *Leu168Val*, *Gly192Ser*, *Thr239Met*, and *Ileu259Val* (Table 2).

The other 2 nonsynonymous variable sites reported were: *Val80Ileu* (N = 1) and *Leu237Ileu* (N = 1). We did not find any further association between color morphs and these remaining 2 nonsynonymous variable sites.

Discussion

In this study, we showed that the dramatic melanic polymorphism observed in red-footed boobies is strongly associated with 2 point substitutions, *Val85Met* and *His207Arg*, at the *MC1R* gene. We also found a strong association between the degree of melanism and the number of copies of variant *MC1R* alleles. Nazca boobies presented the same genotype as white morph red-footed boobies at sites 85 and 207.

The point substitution at position 85 (*Val85Met*) found in red-footed boobies was previously shown to be associated

Table 1. Distribution of sampled brown, intermediate, and white individuals in each possible genotype at sites 85–207, respectively, in the 4 locations sampled

	Brown			Intermediate			White		
	Met–Arg	Met/Val–His/Arg	Val–His	Met–Arg	Met/Val–His/Arg	Val–His	Met–Arg	Met/Val–His/Arg	Val–His
Genovesa	12	4	0	1	6	0	0	0	22
Darwin	2	3	0	0	9	0	0	0	4
Wolf	9	1	0	4	5	0	0	0	10
Johnston Atoll	1	5	0	0	3	0	0	0	11

Met = methionine, Arg = argenine, Val = valine, His = histidine.

Table 2. Nazca boobies (NZ) nonsynonymous substitutions at the *MC1R* gene as compared with white morph red-footed boobies (RFB)

	55	80	**85**	168	192	**207**	239	259
RFB white	Val	Val	**Val**	Leu	Gly	**His**	Thr	Ile
NZ2	Met	Ile	**Val**	Val	Ser	**His**	Met	Val
NZ5	Met	Ile	**Val**	Val	Ser	**His**	Met	Val

In bold are the sites found to be associated with color morph in RFB. Val = valine, Met = methionine, Ile = isoleucine, Leu = leucine, Gly = glycine, Ser = serine, His = histidine, and Thr = threonine.

with melanic phenotypes in lesser snow geese (Mundy et al. 2004). The *Val85Met* point substitution occurs in the outer part of the second transmembrane domain of the *MC1R* gene (Figure 3), and this region has been shown to affect *MC1R* activity (Majerus and Mundy 2003), which suggests that it is highly likely that this substitution is also responsible for the phenotypic change in red-footed boobies. Lesser snow goose (*Anser c. caerulescens*) and red-footed boobies are only distantly related. Lesser snow geese belong to the order Anseriformes that, along with the order Galliformes, forms a cohort that is a sister group to all other modern birds (including red-footed boobies), the cohort Neoaves (Johansson et al. 2001). Therefore, the congruence between the point substitutions at position 85 at the *MC1R* locus suggests parallel evolution of the melanic haplotype and hence melanism between these 2 distantly related species. In other words, the similar phenotype variations observed in these distantly related species have likely arisen independently but through the exact same change at the *MC1R* gene.

In view of the fact that sites 85 and 207 are in complete linkage disequilibrium in all 4 populations sampled and that both these substitutions are nonsynonymous, causing changes in the amino acid sequence, our data cannot determine which one or if both these substitutions are underlying the phenotypic variation in red-footed boobies. Recombination is the mechanism through which linkage disequilibrium is dissipated, moving the system toward equilibrium (Templeton 2006); thus, our data suggest that there has been no recombination between these 2 sites within the *MC1R* gene in red-footed boobies.

In contrast with red-footed boobies, Nazca boobies are monomorphic and show a plumage pattern very similar to that of white morph red-footed boobies, and therefore, it is not surprising that they were found to have the same genotypes at sites 85 and 207. We also found 6 nonsynonymous substitutions between Nazca and white morph red-footed boobies, which could not be directly linked to any plumage differences between these 2 species; only with a detailed

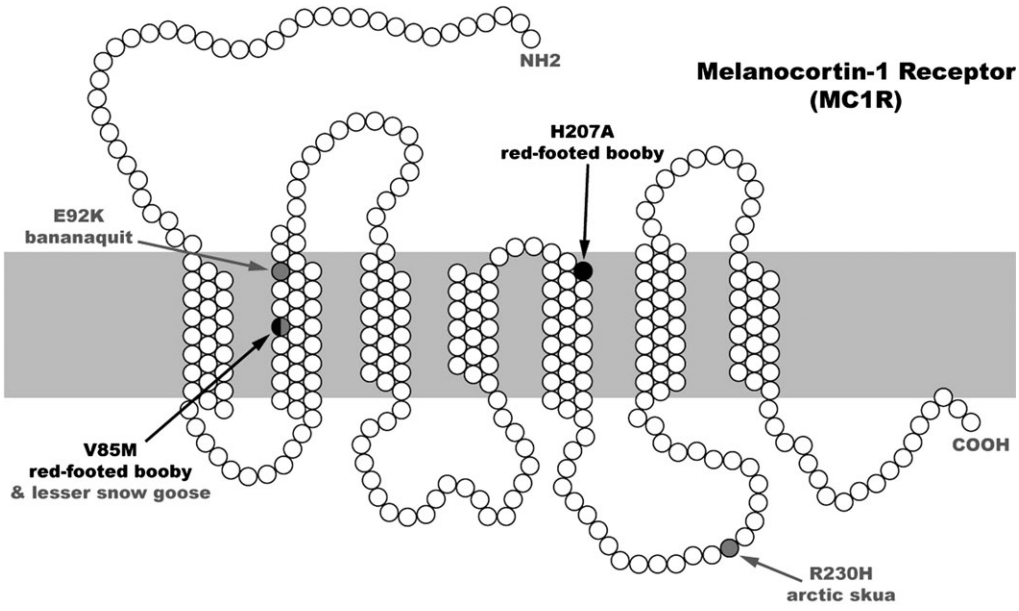

Figure 3. *MC1R* variants associated with plumage changes in wild birds. Extracellular is on the upper part. Black circles represent the amino acid changes found in red-footed boobies. Gray circles represent those changes in wild birds found by other authors (Mundy et al. 2004, lesser snow goose and arctic skua; Theron et al. 2001, bananaquit). Single-letter amino acid code is used to indicate substitutions. Numbers refer to the position of the substitution in the species they represent (illustration after Mundy 2005).

study comparing the *MC1R* sequences of all 6 species in the genus *Sula*, would we be able to elucidate the mechanisms underlying the origin and evolution of these alleles.

It has been shown that the effects of *MC1R* variation on plumage polymorphisms are extremely diverse, causing different patterns of melanism in different species. In bananaquits (*Coereba flaveola*), the substitution at the *MC1R* locus causes a switch from yellow to completely dark birds; in arctic skuas (*S. parasiticus*), changes in the *MC1R* determine gradual changes in the amount of melanin deposited in each feather; finally, in lesser snow geese, variation at the *MC1R* locus correlates with the number of feathers that are melanized. In red-footed boobies, the point substitutions at the *MC1R* locus are related to phenotypes in a similar way to that found in lesser snow geese, decreasing the number of white feathers on the scapular region. These results corroborate the consistency of the association between the substitution at position 85 and phenotypic variation in these 2 species.

The ratio of color morphs is highly variable among islands, being almost reversed in some cases (i.e., Genovesa vs. Johnston Atoll) (Figure 1); if there were effective gene flow among different populations, we would expect a homogenization of the ratio of color morphs in different locations over time. Previous studies have shown that there is maternal gene flow among populations of red-footed boobies in the eastern Pacific Ocean (based on cytochrome *b*) (Steeves et al. 2003); therefore, the fact that different populations have maintained different ratios of color morphs over time may suggest that there is selection acting on the *MC1R* locus, but possible selective pressures have not yet been elucidated. Alternatively, differences in the ratio of color morphs among islands might be better explained by lack of effective gene flow among these different populations instead of differential selection, as suggested by morphometric differences among populations from different geographic locations (Schreiber et al. 1996).

Another possibility is that there is no differential selection between color morphs on different islands, but that instead, the differences in the ratio of color morphs could be explained by the *MC1R* locus being linked to another locus under selection. We also cannot discard other nonadaptive scenarios, such as founder effect, which would predict that populations are dominated by the color morph that first colonized their habitat, with no differential selection on fitness or survival of different color morphs. All these nonadaptive explanations for the observed distribution of plumage morphs are inconsistent with previous descriptions of gene flow among populations in the Eastern Pacific (Steeves et al. 2003); we recommend testing this again at higher molecular resolution.

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