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Skin and Hair Pigmentation Variation in Island Melanesia

Heather L. Norton,[1] Jonathan S. Friedlaender,[2] D. Andrew Merriwether,[3] George Koki,[4]
Charles S. Mgone,[4] and Mark D. Shriver[1]*

[1]*Department of Anthropology, Pennsylvania State University, University Park, Pennsylvania 16802*
[2]*Department of Anthropology, Temple University, Philadelphia, Pennsylvania 19122*
[3]*Department of Anthropology, State University of New York at Binghamton, Binghamton, New York 13901*
[4]*Papua New Guinea Institute for Medical Research, Goroka, Eastern Highlands Province 441, Papua New Guinea*

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ABSTRACT Skin and hair pigmentation are two of the most easily visible examples of human phenotypic variation. Selection-based explanations for pigmentation variation in humans have focused on the relationship between melanin and ultraviolet radiation, which is largely dependent on latitude. In this study, skin and hair pigmentation were measured as the melanin (M) index, using narrow-band reflectance spectroscopy for 1,135 individuals from Island Melanesia. Overall, the results show remarkable pigmentation variation, given the small geographic region surveyed. This variation is discussed in terms of differences between males and females, among islands, and among neighborhoods within those islands. The relationship of pigmentation to age, latitude, and longitude is also examined. We found that male skin pigmentation was significantly darker than females in 5 of 6 islands examined. Hair pigmentation showed a negative, but weak, correlation with age, while skin pigmentation showed a positive, but also weak, correlation with age. Skin and hair pigmentation varied significantly between islands as well as between neighborhoods within those islands. Bougainvilleans showed significantly darker skin than individuals from any other island considered, and are darker than a previously described African-American population. These findings are discussed in relation to prevailing hypotheses about the role of natural selection in shaping pigmentation variation in the human species, as well as the role of demographic processes such as admixture and drift in Island Melanesia. Am J Phys Anthropol 130:254–268, 2006. © 2005 Wiley-Liss, Inc.

The human species shows remarkable variation in both skin and hair pigmentation. Both traits, and particularly skin pigmentation, have commonly been used as a tool to classify individuals into discrete racial groups. However, a closer inspection shows that humans cannot be so neatly categorized. Skin pigmentation, despite often being synonymous with racial taxonomies, shows substantial variation within human populations and within regional groupings or “races.” Pigmentation variation within and among populations has been explained as the result of either natural selection (e.g., Cowles, 1959; Wasserman, 1965; Loomis, 1967; Walter, 1971; Post et al., 1975; Branda and Eaton, 1978; Jablonski and Chaplin, 2000; Mackintosh, 2001) or sexual selection (Darwin, 1871; Diamond, 1988, 1992; Frost, 1988). Selection-based hypotheses have focused on the relationship between skin pigmentation and ultraviolet radiation (UVR) (Walter, 1971; Relethford, 1997; Jablonski and Chaplin, 2000; Chaplin, 2004). High levels of UVR can lead to skin damage such as sunburn or skin cancer, as well as the breakdown of folic acid (Branda and Eaton, 1978). As melanin provides some protection from UVR-induced damage (e.g., Pathak and Fitzpatrick, 1974; Kollias et al., 1991; Sheehan et al., 2002), a compelling selectionist argument is that darkly melanized skin is an adaptation in regions of high UVR. While photodamage and nutrient photolysis may not be very strong selective pressures in regions where UVR is low, these regions present their own challenges. Specifically, it was suggested that lighter pigmentation in these regions may have been an adaptation to ensure the production of sufficient levels of vitamin D_3 in the skin (Murray, 1934; Loomis, 1967). This is a commonly accepted explanation for the general trend toward lighter skin pigmentation in low UVR regions, and recent work by Jablonski and Chaplin (2000) strengthened the case for it.

This paper examines pigmentation variation in Island Melanesia, an equatorial area renowned for its biological and linguistic diversity (Fig. 1). The peopling of Island Melanesia and the larger region of Oceania has been studied from linguistic, archaeological, and biological perspectives. While each of these approaches has revealed particular aspects of the history of human migrations in this region, a synthesis has begun to emerge concerning the outlines of modern human dispersals in Island Melanesia. Human populations had expanded across the Old World and into Australia by 50,000 BP (Roberts et al., 1994; Bowler et al., 2003). The earliest human presence in New Guinea can be dated to at least 40,000 BP, while recent estimates for the earliest occupation of the Bismarck Archipelago (namely New Ireland)

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*Correspondence to: Mark Shriver, Department of Anthropology, Pennsylvania State University, 409 Carpenter Building, University Park, PA 16802. E-mail: mds17@psu.edu

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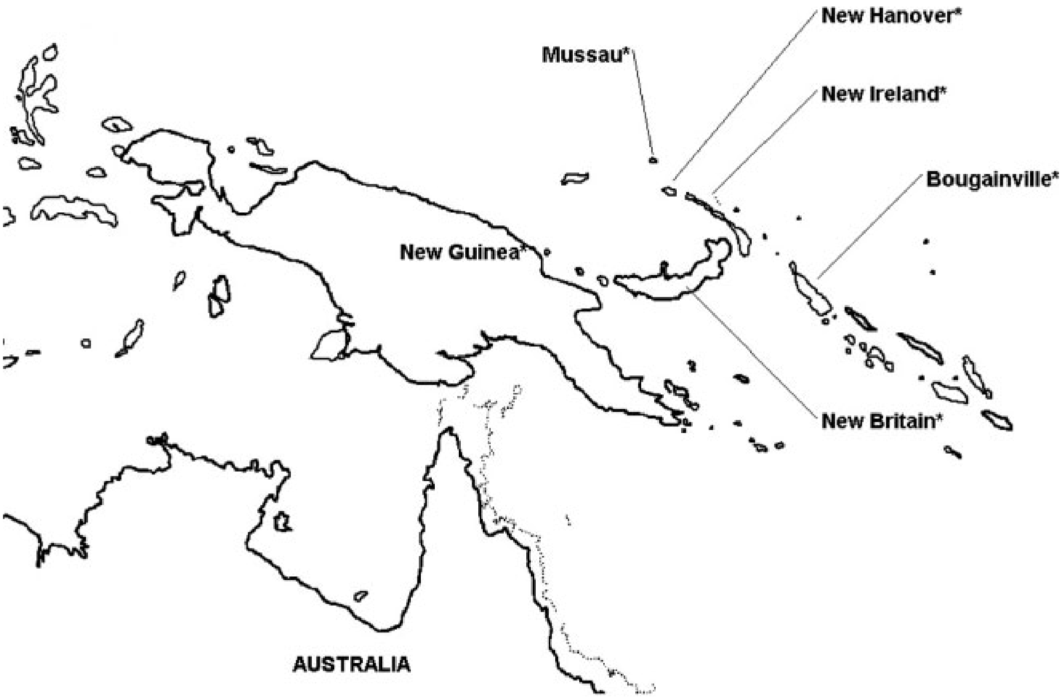

Fig. 1. Map of study region in Island Melanesia. Samples were obtained from islands of New Guinea, New Britain, New Ireland, Mussau, New Hanover, and Bougainville (asterisked).

are also at around 40,000 years BP (Leavesley et al., 2002), implying sailing capabilities at that time. These dates for human occupation at New Ireland suggest an even earlier settlement date for New Guinea, possibly contemporaneous with Australian settlement (Allen, 2003). Evidence for human habitation on the interior of New Britain dates to 35,000 BP (Pavlides and Gosden, 1994), and by 29,000 BP humans had reached Buka and the North Solomons (Wickler and Spriggs, 1988). By 20,000 years ago, archaeological evidence indicates the intentional introduction of animals into the region, as well as more extensive long-range interactions or trade (e.g., Summerhayes and Allen, 1993; Allen 1996; Leaveseley and Allen, 1998). A very distinctive cultural horizon in the Bismarcks dates to about 3,200 years ago, called Lapita, after its distinctive pottery style. It was marked by a number of other novel or intrusive material culture traits, including a number of domesticates (pigs, chickens, and dogs), unique shell ornament types, extensive trading networks, and new settlement patterns, focusing on certain shore locations and peripheral islands (Spriggs, 1995). It was linked to the movement of a new language into the region (Proto-Oceanic, an Austronesian language). This was the ancestor of all the Austronesian languages spoken today throughout Island Melanesia, Polynesia, and most of Micronesia. However, many languages that belong to a non-Austronesian stratum survive, particularly in the interiors of New Guinea and the larger islands of Island Melanesia. Spriggs (1997) hypothesized that the Lapita culture, its extensive trade networks, and the chain of Austronesian dialects that developed with it helped homogenize Island Melanesia during the period 2500–2000 BC, and that subsequently there was a contraction of trade networks and a local diversification of Austronesian-speaking populations in the region. As a corollary to this model, the isolation accompanying these changes would be expected to increase, or at least maintain, genetic diversity across the region.

Earlier genetic studies tended to focus on whether Austronesian (Oceanic)-speaking populations could be distinguished from non-Austronesian (Papuan) ones, or whether simple geographic propinquity in this small region was the best discriminator. The results have been conflicting, although the degree of variation is very high (e.g., Friedlaender, 1975, 1987; Merriwether et al., 1999; Robledo et al., 2004; Friedlaender et al., 2006).

As reported here, pigmentation variation in this region echoes the remarkable genetic diversity observed in previous studies. Although the inhabitants of Island Melanesia are generally darkly pigmented, their skin pigmentation shows a surprising amount of diversity across the region. The explanation for the pattern of diversity within this region cannot be tied directly to contemporary UVR exposure, but rests instead on the history of ancient population migrations or other factors.

MATERIALS AND METHODS

One thousand, one hundred and thirty-five adult individuals from 12 Austronesian- and 6 Papuan-speaking groups from six islands in Island Melanesia were measured for skin and hair pigmentation by H.L.N. and J.S.F. These individuals were measured on New Britain, New Ireland, and New Hanover in the Bismarck Archipelago, and nearby Bougainville. Both Austronesian (AN) and Papuan (P) language-speaking individuals were included. This work was carried out as part of a larger project on the population history and settlement of Island Melanesia. As such, information concerning each individual's age, village of origin, language, and the villages and languages of their parents was also collected along with a 10-cc blood sample for genetic analysis. All individuals involved in this study gave their informed consent to participate as research subjects. Institutional Review Board (IRB) approval for the pigmentation aspects of this work was obtained from Pennsylvania State University (IRB 00M558-2), Temple University (IRB 99-226), and the Papua New Guinea Medical Research Advisory Committee.

Measurement

Measurements of skin and hair pigmentation were taken using the DermaSpectrometer (Cortex Technology, Hadsund, Denmark), a narrow-band reflectance spectrophotometer. The DermaSpectrometer is designed to estimate concentrations of hemoglobin and melanin, the primary chromophores of the skin, based on the work of Diffey et al. (1984). Both hemoglobin and melanin absorb light at lower wavelengths, with hemoglobin showing peak absorbance in the shorter (green) wavelengths, followed by a sharp dropoff in absorbance in the longer (red) wavelengths (above 650 nm). Melanin, however, absorbs consistently across the visible spectrum. Based on these differences in absorbance, Diffey et al. (1984) proposed that the reflectance of narrow-band light in the red spectrum would result in an estimate of the melanin content of an individual's skin (M index), using the following equation:

$$M = \log_{10}(1/\%\text{ red reflectance}).$$

The M index is useful in studies of pigmentation variation because it measures the amount of skin pigmentation that is due primarily to the effects of melanin, with limited confounding effects from hemoglobin.

Many anthropological studies of skin pigmentation variation used reflectometers such as the Evans Electroselenium Limited (EEL) or Photovolt line of instruments (UMM instruments). These reflectometers measure percent reflectance at different wavelengths by passing light through differently colored filters. For example, skin pigmentation studies were commonly performed using red, green, and blue filters (425, 545, and 685 nm for the EEL, respectively). Percent reflectance in the red filter (685 nm) is the closest approximation to the DermaSpectrometer's M index, but it should be noted that the results are not directly comparable.

Prior to use, the DermaSpectrometer was calibrated using the white and black standard provided by the manufacturer, and in accordance with recommended practices. Three measurements were taken on the upper inner left and right arms of subjects, following the recommendations of Shriver and Parra (2000). The upper inner arm was selected as the measurement site because it is a region of the body that is generally unexposed to UVR, allowing for a more accurate measurement of constitutive (unexposed) rather than facultative (tanned) skin pigmentation. Three measurements were also taken of the hair at the crown. Cases where hair had been bleached or colored, or was gray or thin, were noted and subsequently excluded from later analysis. The three hair measurements were averaged together to give a mean hair M index value per individual. The six skin measurements were averaged to yield mean skin M index values for each individual. For analysis of pigmentation variation, subjects were classified into categories according to sex, linguistic phylum (Austronesian or Papuan), island, and neighborhood.

Island classification

Individuals were placed into categories according to their geographic region of origin in Island Melanesia. An individual was placed in a particular island category if both he or she and his or her parents were from that island. In some cases, a subject's reported language was used to help determine island placement. For example, recently a group of Kapugu-speakers from the island of Mussau migrated to the town of Kavieng in New Ireland. Individuals measured in Kavieng who identified themselves and their parents as Kapugu speakers but who listed Kavieng as their home were assigned to Mussau Island rather than New Ireland. Individuals with parents from different islands were excluded from island-level analyses. In this way, a total of 1,046 individuals was assigned to the following islands: Bougainville (153), New Hanover (102), Mussau (35), Manus (2), New Britain (491), New Ireland (242), and New Guinea (21). Due to the extremely small number of individuals who could be assigned to the island of Manus, it was excluded from further island-level analyses.

Linguistic classification

As mentioned, considerable work in the Southwest Pacific explored the relationship between genetic and linguistic variation. The work of Giles et al. (1965), which identified clear genetic distinctions between Austronesian and Papuan language-speakers in the Markham Valley on New Guinea, led to investigations of Island Melanesian diversity according to linguistic affiliation (primarily Austronesian- vs. Papuan-language speakers). While later work (e.g., Serjeantson and Gao, 1995; Merriwether et al., 1999) did not find genetic variation following the clear linguistic divisions observed in the Markham Valley, variation in regions such as Bougainville could be seen to be at least partly (but certainly not entirely) related to linguistic affiliation. Specifically, in Bougainville, linguistic distinctions could explain anthropometric variation better than geographic distance alone. The relationship between language and this biological variation may be explained by past isolation between two groups, due to either different arrival times to the region or isolation because of small population size (Friedlaender, 1975, 1987).

To determine if pigmentation also showed an association with linguistic affiliation, individuals were classed as Austronesian (AN) or Papuan (P), acknowledging that the Papuan languages are extremely diverse and do not form a clearly related family. An individual and both parents had to speak languages belonging to the same linguistic phylum to be classified as either P or AN. As with the island classification scheme, individuals with parents speaking languages belonging to different phyla were excluded from AN/P analyses. Table 1 shows the listing of AN and P language groups included in this study, and the number of individuals in each group. The undivided categories of "Austronesian" and Papuan" are comprised of individuals belonging to AN or P language groups where the population sample size was less than 10, as well as those individuals whose parents spoke different languages from the same phylum. We classified Madak of New Ireland as Papuan rather than Austronesian, because Ross (1994) argued it was originally a Papuan language with a subsequent Austronesian overlay. We compared pigmentation between Austronesian and

TABLE 1. Sample composition of Austronesian and Papuan speakers

Austronesian	n	Papuan	n
Kapugu	34	Aita	36
Kove	45	Anêm	55
Kuanua	18	Ata	68
Lavongai	102	Kuot	53
Mamusi	80	Madak	26
Melamela	37	Sepik	11
Nailik	27	“Papuan”	29
Nakanai	115		
Notsi	20		
Saposa	42		
Teop	23		
Tigak	27		
“Austronesian”	132		
Total	702		278

Papuan speakers across the region, as well as specifically within the separate large islands.

Neighborhood classification

It is important to make our sampling rationale explicit. Our objective was to capture traditional patterns of genetic variation in rural regions of the major islands. Therefore, we selected a set of villages that were distributed across major linguistic groups and also across island sections. Of course, accessibility by road or boat and group interest in participation were important factors. In practice, this generally meant focusing on the few Papuan-speaking populations in the region and their immediate Austronesian-speaking neighbors. We also tried to sample at least two villages from different areas within each language group, in order to obtain some measure of within-language group variation. We refer to our resulting samples as coming from different neighborhoods: neither strictly linguistic nor geographically determined, but a combination of the two.

This is a modification of the more intensive sampling strategy used by Friedlaender (1975) in his much earlier survey in a section of Bougainville, where 18 villages were sampled along a single path that crossed a number of different language groups. In that study, marital migration distances were found to be extremely low for both men and women (typically less than 1 km). Language boundaries appeared to have a very slight additional effect on restricting contemporary marital migration rates, but some biological differences among villages still reflected linguistic distinctions. Friedlaender (1975) argued that this was because language affinity was often a strong indication of long-standing population relationships. We decided this justified using a combination of geographic and linguistic considerations in our sampling of neighborhoods.

Neighborhood classification was carried out in a manner similar to that for linguistic phyla and regions: an individual and both of his or her parents needed to be from the same neighborhood (i.e., same language and residential area) in order to be assigned to that group. In this manner, 829 individuals could be classified into 65 neighborhoods. However, many of these neighborhoods were not used because of insufficient numbers, and we included only those populations for which 10 or more individuals were present in our sample (resulting in 28 neighborhoods, totaling 796 individuals). In 306 cases, an individual and his or her parents identified with different neighborhood groups (implying some difference in language and residential area). These individuals were excluded from neighborhood-level analysis.

Latitude/longitude classification

Many hypotheses about the global distribution of skin pigmentation variation focused on the relationship between pigmentation and UVR. Until recently, it was difficult to directly measure UVR, and latitude was used as a proxy (Roberts and Kahlon, 1976; Tasa et al., 1985; Relethford, 1997). In an effort to explore this relationship, as well as to explore general geographical trends in pigmentation across our relatively small study region, we attempted to assign latitude and longitude coordinates to each individual, based on his or her village of origin. These assignments were made with the help of the online mapping resource, Global Gazetteer version 2.1, found at http://www.fallingrain.com/world/PP/. In some cases, an individual's village could not be found in these sources, although a village known to be nearby was present. In these cases, an individual was assigned the geographic coordinates of the nearby village. In this way, 990 individuals could be assigned latitude and longitude values with confidence.

Recently, the development of remote sensing technologies has provided an opportunity for more direct measurement of UVR. Jablonski and Chaplin (2000) used data from the NASA total ozone mapping spectrometer (TOMS) to examine the relationship of UVR and skin reflectance directly. Although these researchers observed strong correlations with latitude and skin reflectance measured at various wavelengths, they also observed stronger correlations between UVR (measured as the minimum erythemal dose, or UVMED) and skin reflectance at certain wavelengths when examining data from the Northern and Southern hemispheres. The advantage of using information such as that found in the NASA TOMS data set is that it provides a direct measure of UVR. Although latitude and UVR are highly correlated, variation in cloud cover, altitude, or humidity may confound this relationship in localized regions. The effects of using latitude rather than a direct measure of UVR in this study will be discussed below.

Statistical analysis

Mean and standard deviations for hair and skin M index values were calculated for males and females, linguistic phyla, islands, and neighborhoods. Standard two-sample *t*-tests were used to compare pigmentation between males and females as well as between linguistic phyla. In the case of unequal variances, Satherwaite's corrected *t*-statistic was used. To control for sex-based differences in skin and hair pigmentation, skin and hair M index values were z-standardized for sex. With the exception of actual male-female comparisons, all statistical analyses were carried out using these standardized means, unless otherwise noted.

Differences between the group means of islands and neighborhoods were assessed using standard one-way analysis of variance (ANOVA). ANOVA was also used to compare neighborhood means at the island and phylum levels. Pairwise comparisons of neighborhoods within islands and phyla were carried out as *t*-tests, with a Bonferonni correction for multiple comparisons. Interaction effects between categorical and continuous variables in this study were also tested. The relationships between age, latitude, and longitude and pigmentation were assessed using a standard linear regression model. All statistical analyses were performed using the SAS 9.1 software package.

RESULTS

Sex-based differences

The results of standard two-sample *t*-tests comparing skin and hair pigmentation between males and females revealed that males are very highly significantly darker than females (male skin M index = 74.0, female skin M index = 71.2, $P < 0.0001$). Males were also darker than females in hair pigmentation (male hair M index = 155.4, female hair M index = 151.2), although the value did not attain statistical significance ($P < 0.0537$). The significant differences between males and females in skin pigmentation and the near-significant differences between males and females in hair pigmentation prompted the standardization of skin and hair M index values for sex, to avoid sex-related confounding of results. We also examined skin and hair pigmentation differences between males and females within phyla and islands. These results will be discussed below.

Effects of increasing adult age

After standardizing for sex differences, mean hair M index was shown to decrease very slightly, but significantly ($R^2 = 0.0541$, $P < 0.0001$, 2.5% of total variation), with increasing adult age, while skin pigmentation increased fractionally, but significantly ($R^2 = 0.0281$, $P < 0.0001$). We also examined the relationship between age and pigmentation separately for males and females. Males showed a slightly stronger negative correlation between hair pigmentation and age after adulthood ($R^2 = 0.1139$, $P < 0.0001$) than females ($R^2 = 0.0106$, $P < 0.05$). When looking at skin pigmentation, however, females showed a stronger correlation with age ($R^2 = 0.0873$, $P < 0.0001$) than males ($R^2 = 0.0060$, P = NS). In all cases, however, these age effects are weak, and although statistically significant may be of only marginal biological significance.

Linguistic phylum

There was no significant difference between AN and P speakers in terms of skin M index, although the two groups were highly significantly different for hair M index ($t = 3.81$, $P < 0.01$). Comparisons of males and females within each phylum revealed significant differences in skin M between AN males and females (female skin M index = 70.1, male skin M index = 75.1, $P < 0.0001$). No significant differences between Papuan males and females were observed for either skin or hair M index. Mean M index values for males and females within each phylum are shown in Table 2.

Pigmentation of AN and P speakers was compared within each island. AN and P neighborhoods differed significantly from each other in hair pigmentation on both Bougainville ($t = 6.40$ $P < 0.0001$) and New Ireland ($t = 2.39$, $P < 0.05$). AN and P speakers were significantly different for skin pigmentation on New Ireland alone ($t = 2.93$, $P < 0.01$).

TABLE 2. Mean skin and hair M index values for males and females in each linguistic phyla

		Skin M index			Hair M index		
Phylum	Sex	n	Mean	SD	n	Mean	SD
Austronesian	F	331	70.1*	9.7	331	154.0	17.9
	M	374	75.1*	10.8	374	156.2	10.8
Papuan	F	94	74.1	10.6	94	147.8	21.1
	M	184	74.5	11.3	184	151.4	19.0

* Significant male/female difference at $P < 0.0001$.

In addition to testing for differences between AN and P groups, we also tested to see if there was homogeneity in skin and hair pigmentation within the AN and P linguistic phyla. To do this, we compared skin and hair M index values among the 19 Austronesian-speaking neighborhoods and 9 Papuan-speaking neighborhoods (Table 3). Significant differences were found among Austronesian neighborhoods for both skin and hair (skin, F = 37.30, df = 18, $P < 0.0001$; hair, F = 4.40, df = 18, $P < 0.0001$). Papuan neighborhoods showed similar heterogeneity (skin, F = 35.74, df = 8, $P < 0.0001$; hair, F = 7.91, df = 8, $P < 0.0001$). However, much of this variation may be explained by variation between islands (see below). To address this, we used ANOVA to compare mean pigmentation of neighborhoods within each phylum on an island-by-island basis (Table 3). There was significant variation for both hair and skin pigmentation within New Britain's Austronesian- and Papuan-speaking neighborhoods. Significant skin pigmentation variation also existed between Austronesian-speaking groups on Bougainville. These results suggest that heterogeneity exists within AN- and P-speaking groups in the large islands of New Britain and Bougainville, but not for the smaller (and much narrower) island of New Ireland. This emphasizes the importance that island size and geographic complexity can have in maintaining and increasing genetic diversity. This inference is consistent with data from mtDNA and from the non-recombining portion of the Y (NRY) in this same region (e.g., Merriwether et al., 1999; Robledo et al., 2004; Scheinfeldt et al., 2004; Friedlaender et al., in press).

Island

Mean hair and skin M index values for each island, as well as for each major neighborhood within those islands, are shown in Table 4. Mean pigmentation for skin and hair was compared across the six major islands in our study, using ANOVA (Table 3). Islands are significantly different for both hair M index (F = 3.88, df = 5, $P < 0.01$) and skin M index (F = 222.23, df = 5, $P < 0.0001$). Since the Bougainville skin pigmentation results are most distinctive from the other islands ($P < 0.0001$ for all pairwise comparisons), and might therefore be the sole reason for the significant interisland difference, we reran the analysis excluding Bougainville. Even after this exclusion, the remaining islands were significantly different in skin pigmentation (F = 68.47, df = 4, $P < 0.0001$).

Mean skin and hair pigmentation values for males and females on each island are shown in Table 5. Significant differences in skin M between males and females were observed on all islands but New Hanover. Significant differences in hair M index were only found on the island of New Britain.

In an effort to determine if pigmentation is homogeneous within islands, or if heterogeneity among the different neighborhoods on those islands exists, we also used ANOVA to compare mean pigmentation among neighbor-

TABLE 3. ANOVA results comparing islands, neighborhoods, neighborhoods within phyla, and islands

	Skin			Hair		
Model	F	df	*P*	F	df	*P*
Island	222.23	5	0.0001	3.88	5	0.0017
Neighborhoods (entire sample)	35.15	27	0.0001	6.02	27	0.0001
Neighborhoods (within phyla)						
AN	37.30	18	0.0001	4.40	18	0.0001
P	35.74	8	0.0001	7.91	8	0.0001
Neighborhoods within islands						
New Britain	3.92	12	0.0001	8.74	12	0.0001
New Hanover	0.19	2	0.8383	1.00	2	0.3712
New Ireland	2.53	5	0.0316	1.79	5	0.1199
Bougainville	5.25	3	0.0022	18.81	3	0.0001
Neighborhoods within phyla within islands						
New Britain AN	4.28	8	0.0001	7.64	8	0.0001
New Britain P	4.06	3	0.0088	16.12	3	0.0001
New Hanover AN	0.19	2	0.8383	1.00	2	0.3712
New Ireland AN	1.53	2	0.2233	1.70	2	0.1910
New Ireland P	1.18	2	0.3126	0.40	2	0.6749
Bougainville AN	4.87	2	0.0111	2.46	2	0.0977

TABLE 4. Mean skin and hair M index values for islands and neighborhoods[1]

		Skin M index			Hair M index		
Island	Neighborhood	n	Mean (raw)	SD (raw)	n	Mean (raw)	SD (raw)
PNG		21	−0.552 (67.9)	0.302 (9.4)	19	0.816 (160.1)	0.838 (15.3)
	Sepik	11	−0.418 (69.4)	0.967 (10.6)	10	0.869 (169.7)	0.679 (11.7)
New Britain		491	−0.513 (67.9)	0.041 (6.8)	476	0.625 (155.2)	0.960 (17.7)
	Arimegi Island (Kove)	45	−0.761 (65.0)	0.467 (5.3)	41	0.207 (157.5)	0.601 (11.0)
	Kariai (Anêm)	25	−0.021 (72.2)	0.713 (7.5)	25	−0.175 (150.4)	0.473 (8.6)
	Pureling (Anêm)	29	−0.627 (67.1)	0.681 (7.2)	25	−0.388 (147.5)	0.733 (13.2)
	Kisiluvi (Mamousi)	34	−0.274 (69.7)	0.569 (6.6)	32	0.103 (155.3)	0.886 (15.9)
	Lingite (Mamousi)	22	−0.388 (68.6)	0.593 (6.9)	22	0.363 (160.0)	0.873 (16.0)
	Welu (Mamousi)	11	−0.537 (67.3)	0.480 (5.2)	11	0.196 (157.5)	0.769 (13.2)
	other Mamousi	13	−0.530 (67.3)	0.704 (6.5)	13	0.363 (160.6)	0.971 (16.9)
	Loso (Nakanai)	17	−0.237 (70.3)	0.589 (5.5)	17	0.355 (160.2)	1.683 (29.7)
	Uasilau (Ata)	44	−0.547 (67.4)	0.543 (5.4)	44	−0.210 (150.2)	0.775 (14.2)
	Lugei (Ata)	20	−0.492 (67.6)	0.970 (9.7)	19	1.075 (173.3)	1.050 (18.2)
	Bileki (Nakanai)	96	−0.675 (65.7)	0.535 (6.2)	93	−0.507 (144.4)	0.665 (12.2)
	Ubili (Melamela)	36	−0.283 (69.3)	0.661 (6.6)	36	0.661 (165.0)	1.079 (20.2)
	Kuanua (Total)	18	−0.387 (68.3)	0.664 (6.3)	18	−0.076 (151.9)	1.08 (20.4)
Mussau		35	−0.723 (65.5)	0.684 (7.9)	33	0.448 (162.5)	0.544 (10.0)
	Kapugu	34	−0.728 (65.0)	0.662 (7.4)	32	0.495 (162.4)	0.563 (10.1)
New Hanover		102	0.433 (77.1)	0.705 (7.5)	98	0.018 (154.4)	0.856 (16.1)
	North Lavongai	73	0.501 (76.9)	0.685 (6.9)	69	0.109 (154.9)	0.854 (15.9)
	West Lavongai	10	0.379 (75.5)	0.776 (7.6)	10	0.251 (157.3)	0.968 (18.4)
	South Lavongai	13	0.408 (77.3)	0.889 (9.9)	13	−0.217 (150.3)	0.837 (14.2)
New Ireland		242	0.111 (74.2)	−0.152 (8.1)	222	0.724 (151.6)	1.264 (23.1)
	Tigak	27	−0.009 (72.6)	0.704 (8.4)	26	0.15 (156.4)	0.911 (15.9)
	Nailik	26	−0.061 (71.9)	0.573 (6.4)	20	−0.277 (148.9)	1.671 (29.8)
	Kabil (Kuot)	41	0.329 (76.2)	0.709 (7.8)	38	0.349 (147.4)	1.057 (19.1)
	Lamalaua (Kuot)	11	0.153 (75.0)	0.607 (6.2)	9	−0.755 (141.3)	1.72 (29.5)
	Notsi	21	0.286 (74.8)	0.852 (9.0)	20	0.435 (160.8)	1.002 (18.4)
	Madak	26	0.462 (78.0)	0.878 (8.9)	26	−0.205 (148.0)	1.447 (27.5)
Bougainville		153	1.552 (89.8)	0.857 (9.5)	127	−0.205 (150.7)	0.809 (14.6)
	Saposa Island (Saposa)	41	1.283 (86.1)	0.905 (9.9)	29	0.044 (154.3)	0.636 (11.4)
	Inivus (Teop)	10	2.052 (93.1)	0.807 (9.0)	9	0.616 (164.5)	0.660 (11.6)
	Sunahoara (Teop)	10	1.977 (94.6)	0.524 (6.5)	9	0.228 (158.5)	0.695 (12.0)
	Kukuavo (Aita)	32	1.901 (91.9)	0.734 (8.5)	30	−0.821 (138.6)	0.538 (8.9)

[1] Islands include individuals belonging to neighborhoods listed below each island heading, as well as individuals who could not be assigned to a particular neighborhood within an island. Papuan-speaking neighborhoods are in bold.

hoods on the islands of New Hanover, New Britain, New Ireland, and Bougainville, the four islands containing multiple neighborhoods (Table 3). We observed significant variation in hair pigmentation on the islands of Bougainville (F = 18.81, df = 3, $P < 0.0001$) and New Britain (F = 8.74, df = 12, $P < 0.0001$). Significant variation in skin pigmentation was present on New Ireland (F = 2.53, df = 5, $P < 0.05$), New Britain (F = 3.92, df = 12, $P < 0.0001$), and Bougainville (F = 5.25, df = 3, $P < 0.01$).

Neighborhood

Neighborhoods are significantly different for hair (F = 6.02, df = 27, $P < 0.0001$) as well as skin pigmentation

TABLE 5. Mean skin and hair M index values for males and females on each island

		Skin M index			Hair M index		
Island	Sex	n	Mean	SD	n	Mean	SD
PNG	F	6	60.6*	6.9	5	154.9	19.3
	M	15	70.9*	8.8	14	162.0	13.9
New Britain	F	190	66.0***	6.9	186	152.5*	19.7
	M	301	69.2***	6.5	290	156.9*	16.0
New Hanover	F	61	76.1	6.5	60	153.4	16.9
	M	41	78.6	8.7	38	155.9	14.7
Mussau	F	17	61.3*	6.2	17	162.4	10.4
	M	18	69.5*	7.4	16	162.7	9.9
New Ireland	F	118	71.5***	7.4	111	152.6	23.5
	M	124	76.8***	7.8	111	150.6	22.7
Bougainville	F	62	86.6**	8.4	59	150.5	13.8
	M	91	92.1**	9.7	68	150.8	15.4

* Significant male/female difference at $P < 0.05$.
** Significant male/female difference at $P < 0.001$.
*** Significant male/female difference at $P < .0001$.

(F = 34.96, df = 27, $P < 0.0001$). Again, thinking that the extremely dark-skinned Bougainvilleans might be influencing these results, we reran the analysis without the four Bougainville neighborhoods. After the exclusion of these neighborhoods, there was still significant evidence for differences in mean pigmentation among neighborhoods for both hair (F = 5.46, df = 23, $P < 0.0001$) and skin (F = 13.99, df = 23, $P < 0.0001$). Although this is likely influenced by between-island differences in pigmentation, the comparison of neighborhoods within islands (see above) demonstrates that these differences can be found even within islands.

Table 6 contains mean skin and hair pigmentation values for males and females in each of the 28 neighborhoods. In many cases, samples sizes are too small to conduct *t*-tests of between-sex differences. However, the general trend of darker males relative to females is still evident.

Latitude and longitude

Latitude was not statistically related to hair ($R^2 = 0.0003$, $P < 0.5937$) or skin ($R^2 = 0.0000$, $P < 0.9805$) pigmentation, nor is there any suggestion of any such underlying tendency. The lack of a strong correlation between latitude and skin pigmentation here should not be seen as a contradiction of the well-documented associations found across broader regions. In this sample, we have a very small range in tropical latitude (9.3°), and are using this as a proxy for UVR to test for its association with very large differences in pigmentation. If we restrict our analysis to only those samples from Island Melanesia proper (excluding Papua New Guinea), we are looking at an even smaller range (1–7° latitude). One cannot expect very long-term differential selection effects to result in well-defined clines in small regions with histories of small population sizes and a series of in-migrations, combined with considerable isolation.

As a further illustration of this apparent contradiction, longitude does show some statistical association with pigmentation across our sample. Although the relationship between longitude and hair pigmentation was statistically significant ($P < 0.05$), it is extremely weak ($R^2 = 0.0057$). However, the relationship between skin pigmentation and longitude was quite strong ($R^2 = 0.3511$, $P < 0.0001$), with pigmentation increasing from west to east across the study region. As Bougainville has the highest mean skin pigmentation of any of the islands surveyed, and also lies at the extreme east of our study region, we suspected that the inclusion of Bougainville in the analysis might explain this strong west-east cline in pigmentation values. When the analysis was rerun without the Bougainvilleans, we found that the correlation between longitude and pigmentation decreased dramatically, although it retained statistical significance ($R^2 = 0.0279$, $P < 0.0001$).

Interaction effects

We also tested for interaction effects between our categorical variables of phylum, island, and neighborhood and the continuous variables age, latitude, and longitude. In these models, we tested both the main effect of the continuous and categorical variables in question, but also for an interaction effect between the two. At the phylum level, significant interactions between phylum and longitude were observed for both skin (F = 26.4, df = 1, $P < 0.0001$) and hair (F = 12.59, df = 1, $P < 0.001$) pigmentation. Significant interactions between island and latitude (F = 3.35, df = 5, $P < 0.01$) and island and longitude (F = 3.13, df = 5, $P < 0.01$) were observed for skin pigmentation. There were also significant interactions between island and age (F = 5.84, df = 5, $P < 0.0001$) and island and longitude (F = 2.58, df = 5, $P < 0.05$) for hair pigmentation. Hair pigmentation was also influenced by interaction between neighborhood and age (F = 2.55, df = 27, $P < 0.0001$) and neighborhood and longitude (F = 1.64, df = 17, $P < 0.05$).

DISCUSSION

Sex-based differences

When we compared all males and females in this study (irrespective of phylum, island, or neighborhood affiliations), we observed very highly significant sexual dimorphism with respect to skin pigmentation, with males being darker than females ($P < 0.0001$). These differences persisted when we compared males and females within the same island for 5 out of 6 islands. Although sample sizes were often too small to test for significant differences in males and females at the neighborhood level, the general trend of males being darker is apparent. Males also tended to be darker than females for hair pigmentation, although this dimorphism is only of suggestive significance ($P < 0.0537$). The differences that we report in skin M index between males and females are consistent with a number of reports from the literature describing females as significantly lighter than males in most populations (e.g., Barnicot, 1958; Tobias, 1961; Conway and Baker, 1972; Byard and Lees, 1982; Harvey, 1985; reviewed in van den Berghe and Frost, 1986; Frost, 1988). In their review of skin reflectance data, Jablonski and Chaplin (2000) reported a similar pattern. However, Wagner et al. (2002) did not find any such differences in their study of European Americans, Hispanics, or East Asians (although the Hispanic and East Asian sample sizes were small).

The reports of darker males relative to females in a number of studies were explained as due to hormonal differences between males and females or as the result of sexual selection favoring lighter females (Frost, 1988, 1994). Van den Berghe and Frost (1986) suggested that the male/female differences observed in many pigmentation studies are tied to a relationship between the

TABLE 6. Mean skin and hair M index values for males and females in each neighborhood

			Skin M index			Hair M index		
Island	Neighborhood	Sex	n	Mean	SD	n	Mean	SD
PNG								
	Sepik	F	1	47.3		1	178.8	
		M	10	71.6	8.1	9	168.7	11.9
New Britain								
	Arimegi Island (Kove)	F	15	61.5	6.0	14	156.0	15.2
		M	30	66.8	3.4	27	158.4	8.3
	Karaiai (Anêm)	F	12	70.4	7.2	12	149.0	8.4
		M	13	73.8	7.8	13	151.6	8.8
	Pureling (Anêm)	F	3	65.1	10.6	3	132.9	11.8
		M	26	67.3	6.9	22	149.5	12.3
	Kisiluvi (Mamousi)	F	16	65.9	5.3	15	152.0	13.9
		M	18	73.1	5.7	17	158.2	17.4
	Lingite (Mamousi)	F	10	64.1	6.2	10	155.6	18.0
		M	12	72.4	4.9	12	163.6	13.9
	Welu (Mamousi)	F	4	65.1	6.5	4	161.6	9.7
		M	7	68.5	4.3	7	155.1	15.0
	other Mamousi	F	3	73.2	10.0	3	161.3	11.3
		M	10	65.9	4.4	10	160.4	18.7
	Loso (Nakanai)	F	6	71.9	6.1	6	159.9	28.4
		M	11	69.4	5.3	11	160.4	31.8
	Bileki (Nakanai)	F	42	61.4	5.5	42	141.3	12.8
		M	54	69.0	4.5	51	147.0	11.3
	Lugei (Ata)	F	7	70.7	6.0	6	183.6	5.1
		M	13	66.0	10.6	13	168.5	20.2
	Uasilau (Ata)	F	12	68.1	5.5	12	143.0	17.4
		M	32	67.1	5.3	32	152.9	12.1
	Ubili (Melamela)	F	22	69.0	6.9	22	161.3	24.4
		M	14	69.2	6.3	14	171.0	19.9
	Kuanua	F	9	69.9	5.6	9	144.9	26.2
		M	9	66.7	6.8	9	158.8	9.6
Mussau								
	Kapugu	F	17	61.3	6.2	17	162.4	10.4
		M	17	68.6	6.8	15	162.4	10.1
New Hanover								
	North Lavongai	F	48	76.6	6.5	47	152.6	17.2
		M	25	77.5	7.8	22	159.8	11.8
	West Lavongai	F	7	75.5	8.5	7	153.0	20.6
		M	3	75.5	6.7	3	167.4	4.7
	South Lavongai	F	4	71.8	3.6	4	155.8	9.3
		M	9	79.7	11.0	9	147.8	15.8
New Ireland								
	Tigak	F	12	65.7	5.8	12	158.1	11.5
		M	15	78.1	5.6	14	154.9	19.2
	Nailik	F	12	69.2	4.3	9	153.6	32.5
		M	14	74.2	7.2	11	144.9	28.4
	Kabil (Kuot)	F	16	72.5	6.6	16	146.1	21.8
		M	25	78.5	7.8	22	148.4	17.3
	Lamalaua (Kuot)	F	2	75.3	2.8	2	163.8	8.8
		M	9	74.9	6.9	7	134.9	30.4
	Notsi	F	14	72.1	8.7	13	154.5	19.5
		M	7	80.4	7.4	7	172.4	8.5
	Madak	F	12	77.8	8.3	12	150.4	27.9
		M	14	78.2	9.6	14	146.0	28.1
Bougainville								
	Saposa Island (Saposa)	F	15	82.2	7.5	14	153.6	11.7
		M	26	88.4	10.5	15	155.0	11.6
	Inivus (Teop)	F	6	89.8	9.6	5	164.8	8.4
		M	4	98.0	6.0	4	164.2	16.2
	Sunahoara (Teop)	F	1	79.1		1	161.4	
		M	9	96.3	3.8	8	158.1	12.7
	Kukuavo (Aita)	F	17	87.6	8.0	17	140.1	5.9
		M	15	96.7	6.1	13	136.5	11.8

reported decrease of female pigmentation around the time of menarche (Robins, 1991). Since skin pigmentation can increase with age, lighter skin may be seen as a sign of fecundity, causing males to view females with relatively lighter skin as desirable (van den Berghe and Frost, 1986). However, there are few data to confirm or refute the hypothesis that males actually choose their mates based on slight pigmentation differences that are only measurable by instrumentation and not obvious to the human eye.

It is also possible that any differences seen between the sexes are purely the result of different behavioral patterns that affect UVR exposure levels. The observations of darker males in many studies are consistent with the idea that men may experience a greater lifetime UVR exposure, perhaps due to differences in clothing or activity patterns. For example, we observed that the large amount of time spent by men fishing on the ocean in outrigger canoes (where UVR exposure, due to reflectance off the water, would be substantially higher than on land) could dramatically inflate between-sex differences in pigmentation. The result would be an increase in the facultative pigmentation of males relative to females, while constitutive pigmentation should remain the same. While our measurement site was chosen for its relatively low UVR exposure, some researchers suggest that the buttocks may be a more ideal measurement location to avoid seasonal variation in pigmentation that may occur due to facultative tanning (Lock-Andersen and Wulf, 1997).

Age

Hair pigmentation decreased slightly but significantly with age. Individuals noted to have white or graying hair were excluded from this analysis, so the negative relationship between age and hair M index cannot be easily explained by the presence of individuals with severely or obviously depigmented hair in the upper age categories. This suggests that melanin content of the hair does decrease with age, independent of subjectively assessed graying. This may in part be due to the decline with age in the number of melanocytes present in the hair follicle, although this decline is typically associated with an increase in graying (Robins, 1991). It is also possible that some individuals with a small number of gray hairs were included in the analysis. If a gray hair were included in the region measured by the DermaSpectrometer, this could also explain the observed decrease in hair M index with age. This decrease in hair M index was more pronounced among males than among females.

We observed a slight increase in skin pigmentation with age in females ($R^2 = 0.0873$, $P < 0.0001$). Males showed no significant relationship. While many reports in the literature describe changes in pigmentation from birth through adolescence or young adulthood (e.g., Kalla and Tiwari, 1970; Conway and Baker, 1972; Williams-Blangero and Blangero, 1991), some also examined changes in skin pigmentation throughout adulthood. Many of these suggested either no significant relationship between age and skin pigmentation (Harvey and Lord, 1978; Harvey, 1985), or a slight decrease in pigmentation with age (e.g., Conway and Baker, 1972; Frischano et al., 1981). Again, although the inner arm was selected as a measurement site in this study because it is relatively protected from UVR (and was a culturally accepted measurement site, unlike the buttocks), it is still possible that over the course of many years, facultative tanning could result in an overall increase in skin M index at this site. This could result in the weak but positive correlation between pigmentation and age observed here.

Two additional factors could explain these results, however. First, our sample is not equally distributed across all ages: over 80% of individuals in our sample were below age 50. When the analysis is repeated including only individuals younger than age 50 years, the correlation between skin pigmentation and age actually increases ($R^2 = 0.0308$, $P < 0.0001$), although the relationship remains quite weak. Secondly, as we have seen that both skin and hair pigmentation differs significantly among islands, it is possible that the results of our age analysis could also be the result of significant differences in mean age between islands. The mean age of our New Britain sample (32.8 years) is significantly younger than that of all islands except Papua New Guinea ($P < 0.05$, after Bonferonni correction for multiple tests). This may also explain the significant interaction effect between age and island, and age and neighborhood (since neighborhoods are nested within islands), on hair pigmentation. Interestingly, Williams-Blangero and Blangero (1991) found that age-related changes in skin color varied among populations in eastern Nepal, although this study dealt only with age changes in skin pigmentation in individuals aged 3–21 years.

Linguistic phylum

Constitutive pigmentation is under strong genetic regulation, and as such, it was thought that observed differences between Austronesian and Papuan speakers may reflect pigmentation differences between the progenitors of these two groups, assuming there were, in fact, only two progenitor groups. However, studies of genetic variation between these two groups led to conflicting results. For example, although Giles et al. (1965) reported clear distinctions between Austronesian and Papuan speakers for Gm antigens in the Markham Valley of New Guinea, such stark contrasts between the two groups were not found in Bougainville (Friedlaender and Steinberg, 1970) or in the coastal region of Madang in New Guinea (Serjeantson and Board, 1992).

Recent work suggests that the different conclusions about Austronesian/Papuan genetic distinctions may be due in part to different levels of admixture between Austronesian and Papuan speakers in the past. For example, the sharp differences in Gm antigen frequency observed by Giles et al. (1965) may be attributed to a recent arrival of Austronesians to the region, and hence to less time for gene flow to reduce any preexisting differences between the two groups (Friedlaender et al., 2006). Studies where genetic differences between the two groups were observed to be less distinct may reflect greater amounts of admixture between the two groups. The adoption of a neighboring group's language may also have helped to blur biological distinctions between these groups, as in the case of Madak. Another questionable factor in these comparisons is the presumed original homogeneity of Austronesians and (especially) Papuans.

We did not observe significant differences between Austronesian and Papuan speakers in skin pigmentation, although the two groups were significantly different for hair pigmentation. Comparisons of AN and P speakers within the three islands for which we had samples of both groups (New Britain, New Ireland, and Bougainville) revealed significant differences in hair pigmentation on Bougainville and New Ireland. New Ireland was the only island to show significant differences between the two groups in skin pigmentation.

Our analyses demonstrated significant differences in skin and hair pigmentation between the AN and P neighborhoods in this study. After controlling for interisland differences in pigmentation, we found evidence for heterogeneity in hair and skin pigmentation among the AN- and P-speaking neighborhoods of New Britain, and in skin pigmentation among AN-speaking neighborhoods of Bougainville.

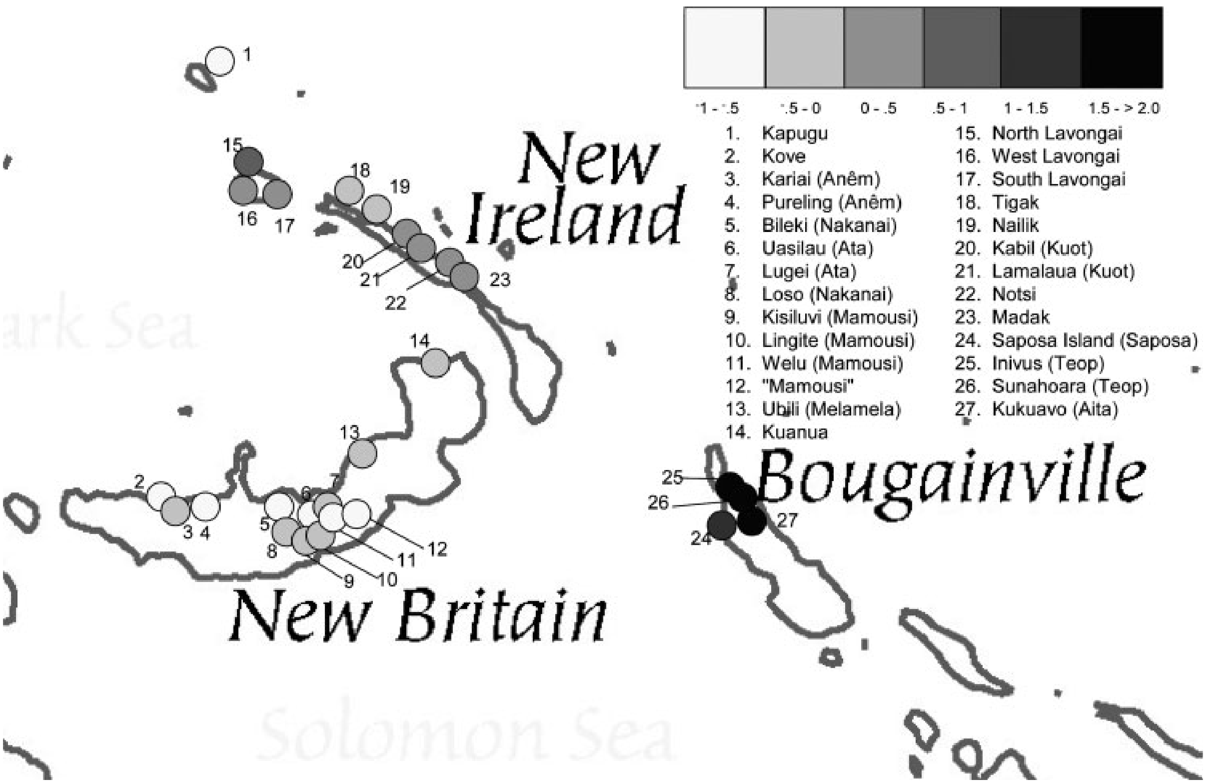

Fig. 2. Skin M index for 27 of 28 populations reported in this study (Sepik of New Guinea are not included). Intensity of circle marking each population on map corresponds to pigmentation as measured by M index.

The fact that no significant within-island variation in skin pigmentation was found between Austronesian and Papuan speakers in Bougainville and New Britain suggests that perhaps sufficient admixture has occurred between the two groups to blur any original skin pigmentation differences that may have existed. The significant difference in skin pigmentation between the two groups on New Ireland is especially interesting, given the debated status of the Madak language as belonging to either the AN or P phylum. Ross (1994) believed that the Madak language, while traditionally being classified as AN, has an underlying structure that suggests that it was at one time a Papuan language. Over a period of time, these proto-Madak speakers may have adopted features of the AN languages of their neighbors on New Ireland. Such conversions are also expected to be accompanied by gene flow between the two groups (Dutton, 1995). When the analysis is performed with Madak as an AN language, no significant differences between AN and P speakers are found in NI for either skin or hair pigmentation. As a group, Madak speakers represent the darkest people on New Ireland (M index = 78.0), and they also have the second-lowest M index values for hair (M index = 148.0; the two Papuan-speaking Kuot groups from Kabil and Lamalaua in our sample are the lightest, with a mean hair M index of 146.2). The fact that Madak speakers are more similar to the one clear Papuan-speaking group on New Ireland than they are to AN speakers suggests that they may have a more recent shared ancestry with P-speaking groups such as the Kuot. It also suggests that the language conversion occurred fairly recently. It will be of great interest to compare the genetic variation of Madaks to other AN and P groups in New Ireland.

Bougainville is the only other island on which significant AN/P pigmentation differences were detected. In this instance, only hair pigmentation differed between groups. The variation in hair M index on Bougainville can be largely attributed to the lighter hair of the Papuan-speaking Aita from Kukuavo (M index = 138.1) relative to the darker Austronesian-speaking Saposa (M index = 153.7) and Teop speakers from Inivus and Sunahoara (pooled M index = 162.0). Pairwise comparisons reveal that the Kukuavo are significantly different from all other Bougainvillean neighborhoods in hair pigmentation ($P < 0.0001$). The Aita, until recently, were a relatively isolated group in the northern mountains of Bougainville, and are notable for lacking the mtDNA 9-bp deletion (often associated with the "Polynesian motif") that characterizes all Austronesian populations (Merriwether et al., 1999), as well as some Papuan-speaking groups (including those of southern Bougainville).

We observed significant interaction effects for both skin and hair pigmentation between the variables phylum and longitude. As we have already noted, Bougainville is unique in that it lies at the extreme east of our distribution, and also has the darkest mean skin pigmentation. In addition, the Papuan-speaking Aita of Bougainville are notable for their very light hair. When Bougainvilleans are excluded, there is no significant interaction effect between phylum and longitude for either skin or hair pigmentation.

Island and neighborhood variation

Skin and hair pigmentation varied significantly at both the island and neighborhood levels. Figure 2 shows skin M index variation for 27 of the 28 neighborhoods studied (the Sepik of New Guinea were excluded from the map for clarity). The five islands shown can be clearly distinguished by skin M index, despite some internal variation within these islands. The island with the lightest-skinned inhabitants is Mussau, located to the north of New Hanover and near the equator at latitude −1.4°. Individuals from New Guinea (not shown; mean skin M index = 67.9) and New Britain are also relatively lightly pigmented. Skin pigmentation increases in New Hanover and New Ireland, and increases again in Bougainville. The Bougainvilleans (mean skin M index = 89.8) are so dark compared to other groups in this study (mean skin M index = 70.6) that they were removed from the island-level analysis to determine if skin pigmentation still varied significantly among the remaining regions. Despite this, pigmentation differences among islands remained highly significant.

Significant variation in skin pigmentation among the 28 major neighborhoods was also observed. Neighborhoods from Bougainville were notably darker than populations from all other islands. When these Bougainvillean groups are excluded from the neighborhood-level analysis, neighborhoods still vary significantly with respect to both skin and hair M index. The heterogeneity within islands is consistent with the significant interaction effects observed for island and latitude and island and longitude. As such, it is not only *which* island an individual is from, but *where* on that island.

Although there was significant variation in skin pigmentation among the islands studied, significant within-island variation among neighborhoods was also observed for Bougainville, New Britain, and New Ireland. This suggests that while regional distinctions in pigmentation may be important, homogeneity within those regions is not necessarily the norm. Studies such as those of Robledo et al. (2004) and Merriwether et al. (1999) suggest that genetic variation within and between large islands follows a similar pattern.

Despite the large amount of variation in skin pigmentation in Island Melanesia, the inhabitants are darkly pigmented relative to other populations such as European Americans (mean skin M index = 29.5) and East Asians (mean skin M index = 32.6) and African Americans (mean skin M index = 53.4) and African Caribbeans (mean skin M index = 57.8) (Wagner et al., 2002; Shriver et al., 2003). This dark pigmentation is consistent with two of the many selection-based hypotheses regarding variation in human skin pigmentation. The first of these, the photoprotection hypothesis, is based on studies of the protective properties of melanin against UVR-induced damage such as sunburn and skin cancer (e.g., Pathak and Fitzpatrick, 1974). Specifically, protection provided by highly melanized skin would eliminate or minimize the painful effects of sunburn, and reduce the risk of skin cancer.

The second major natural selection-based hypothesis regarding normal variation in human skin pigmentation is also dependent on the photoprotective effects of melanin. Hibbard and Smithells (1965) reported an association between fetal abnormalities and folate deficiencies. Later work sought to demonstrate a link between folate deficiencies and neural-tube birth defects, as well as to demonstrate the effectiveness of folic acid supplementation at decreasing the risk of such defects (e.g., Smithells et al., 1980; Laurence et al., 1981; Bower and Stanley, 1989; MRC Vitamin Study Research Group, 1991; Czeizel and Dudas, 1992). The folic acid hypothesis (Branda and Eaton, 1978) suggests that there is strong selection pressure to maintain a darkly pigmented skin in tropical regions to avoid the breakdown of folic acid and other metabolites via UVR exposure, and hence an increase in neural-tube birth defects (Jablonski, 1992) as well as nondisjunction errors during spermatogenesis (Mathur et al., 1977). Flemming and Copp (1998) identified a link between folate deficiency and neural-tube birth defects in the mouse, creating renewed interest in this hypothesis (e.g., Jablonski and Chaplin, 2000).

A third major hypothesis dealing with the evolution of human skin pigmentation variation is the vitamin D hypothesis (Loomis, 1967). However, as this hypothesis focuses mainly on the effects of positive selection for low melanin content in populations of higher latitudes, it is not pertinent to the populations under study here. It can be noted, however, that the predictions of the vitamin D hypothesis are not inconsistent with darkly pigmented skin in regions of high UVR.

While there are other hypotheses regarding human pigmentation variation, these are the three to receive recent attention (Jablonski and Chaplin, 2000; Relethford, 1997). It should also be noted that these hypotheses are not necessarily mutually exclusive: it may be that all three together have helped shape the global distribution of skin pigmentation. The suggestion of both Darwin (1871) and Diamond (1988) that sexual selection may also play a role in shaping human pigmentation variation should also not be ignored, although this idea is not testable using these data.

As predicted by the photoprotection and folic acid hypotheses, inhabitants of Island Melanesia do indeed have darkly pigmented skin, although there is a substantial amount of variation. It is possible that with respect to these two hypotheses, there is a certain "melanin threshold" of skin pigmentation that represents a level of adaptive pigmentation in a high UVR region. Individuals below that threshold are not well-protected from UVR-induced photodamage to the skin or folic photolysis. Once that threshold is crossed, selection ceases to be a strong force in constraining variation in skin pigmentation. Under this scenario, pigmentation above a certain level would not be a target of selection, while pigmentation below that level could be related to fitness. This may help explain why, although in general darkly pigmented, Island Melanesians show such extreme variation. A related concept was proposed by Chaplin (2004). Chaplin (2004) suggested that there may be a point at which it is simply not possible for pigmentation to increase. As humans near this melanin maximum, adaptation (in terms of melanin increase) should become increasingly slower. Rather than saying that Island Melanesians are bumping against this upper melanin boundary, we argue that as long as pigmentation is maintained above a certain protective level, individuals may vary in pigmentation with no (or minimal) negative effects on fitness. Certainly it is possible that under this scenario, some groups may approach the maximum of Chaplin (2004); Bougainvilleans are a possible example.

An alternative is that the variation within the region that we observe is actually directly related to variation in UVR levels or to a population's duration of habitation in a particular UVR environment. Under this scenario, this variation may represent extremely localized adaptations to very specific environmental conditions. While we strongly believe that natural selection has shaped mean pigmentation levels in the region, our results are most consistent with the "melanin threshold" model, and we propose that variation within the region has been more strongly influenced by the population histories of these groups.

The variation in skin pigmentation we observe is consistent with the population history of the region and patterns of isolation and migration over the past few millennia. Reproductive isolation of these populations from one another may have led to differentiation in pigmentation at both the island and neighborhood levels. This process could be the result of random genetic drift, founder effect, and differential gene flow, as well as possible localized sexual selection acting on pigmentation phenotype. While it is unlikely that these groups have remained completely isolated from each other for extensive periods of their histories, even partial isolation may have aided in this differentiation process. Bougainville is particularly interesting from this perspective, because it differs notably from the other regions considered here, and is also the most geographically isolated of the groups.

Our time spent in this region provided some anecdotal evidence for the possibility of localized sexual selection acting in Island Melanesian populations. For example, neighbors of the Anêm-speaking people of West New Britain believed that Anêm women were ugly, and specifically that they had darker skin than themselves. This difference in pigmentation (and hence physical attractiveness) was cited as an argument against intermarriages with the Anêm. Skin reflectance measurements confirm the pigmentation observation (mean skin M index of Anêm women = 69.4; mean skin M index of Kove women = 61.5), but whether or not pigmentation is the driving factor limiting intermarriage with the Anêm remains to be seen. Similarly, in Bougainville, Aita women were described as "disgusting" and darker than their neighbors (no significant difference in skin M index was observed), resulting in a similar claimed avoidance of intermarriage. This is interesting, given that Bougainvilleans in general express a preference for individuals with "clear black" skin, suggesting that perhaps there are other factors behind this avoidance practice. The Aita live in an isolated mountainous region of northern Bougainville, and although the Anêm had recently moved down to the coast, they were originally an inland rather than shore-based group. It may be that the resistance of coastal groups to intermarriage with supposedly "darker" populations such as the Aita or Anêm is really reflective of resistance to intermarriage with inland populations that are generally considered less sophisticated. Whatever the reason, this resistance may help strengthen the genetic differences observed between coastal and inland groups.

While the photoprotective and folic acid hypotheses predict dark pigmentation in tropical regions, it seems as if the dark skin color of Bougainvilleans could not have been strictly controlled by the effects of natural selection alone. If it were, we would expect other Melanesian groups to display pigmentation levels similar to Bougainvilleans. However, the Bougainvilleans as a group are strikingly darker than other Island Melanesians, as well as darker than previously measured African Americans and African Caribbeans, as shown in Figure 3. It should be noted that these African Americans and African Caribbeans are admixed populations, and it is possible that other African or African-derived populations would be more darkly pigmented. Also, African populations should not be considered homogeneous for skin pigmentation. The mean skin M index of 89.8 is remarkable in any context. It is possible that the remarkable pigmentation observed in the Bougainvillean populations was also shaped by either drift and/or sexual selection.

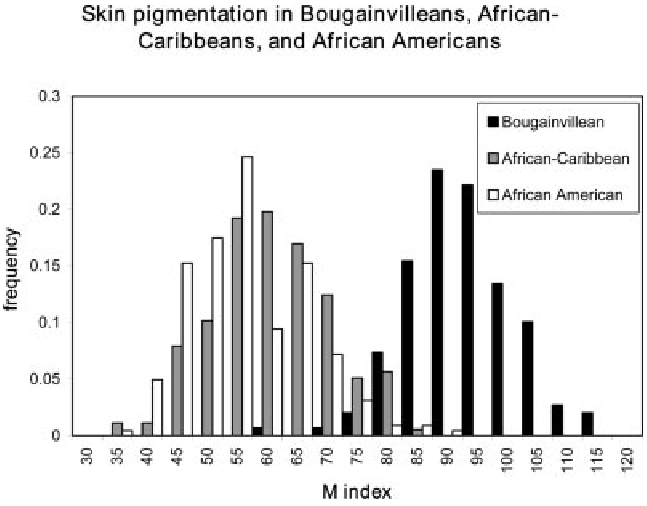

Fig. 3. Distributions of skin M index values for Bougainvilleans measured in this study, and African Americans and African Caribbeans measured by Shriver et al. (2003).

Hair M index variation across populations is distinctly different from variation in skin pigmentation, though still highly variable. Figure 4 shows hair M index values plotted for 27 of the 28 major populations in this study (as before, the Sepik of New Guinea were excluded). Although the islands differ significantly by hair M index, there is also substantial variation among populations within each island, particularly for Bougainville and West New Britain. As with skin pigmentation, we observed a significant interaction effect for island and longitude on hair pigmentation. We feel that this is consistent with the within-island heterogeneity observed for hair pigmentation.

An interesting hair phenotype that is sometimes seen in Island Melanesia (as well as among Australian Aborigines) is "blondism," in which individuals exhibit the characteristic darkly pigmented skin of the region while also having blond hair. This trait was most commonly observed in children whose hair generally darkened around puberty (Robins, 1991). However, in some cases, blondism persists into adulthood, although the hair appears somewhat darker than what is seen in children. The strikingly light hair of the Aita (Fig. 4) is partially due to the high incidence of blondism among this group.

While a large body of work has been devoted to explaining variation in skin pigmentation, especially via natural selection, much less work has been done to explain normal variation in hair pigmentation. It is possible that variation in hair pigmentation is mediated not so much by natural selection as by sexual selection. While no association between skin and hair M index was found in the combined sample ($R^2 = 0.0003$, $P < 0.5641$), it is interesting to consider how natural selection-based constraints on skin pigmentation in this tropical region may have indirectly limited variation in hair pigmentation.

At least some pigmentation candidate genes, such as the melanocortin 1 receptor (*MC1R*), can have an effect on both hair and skin pigmentation. Perhaps if those genes were under functional constraint to maintain a

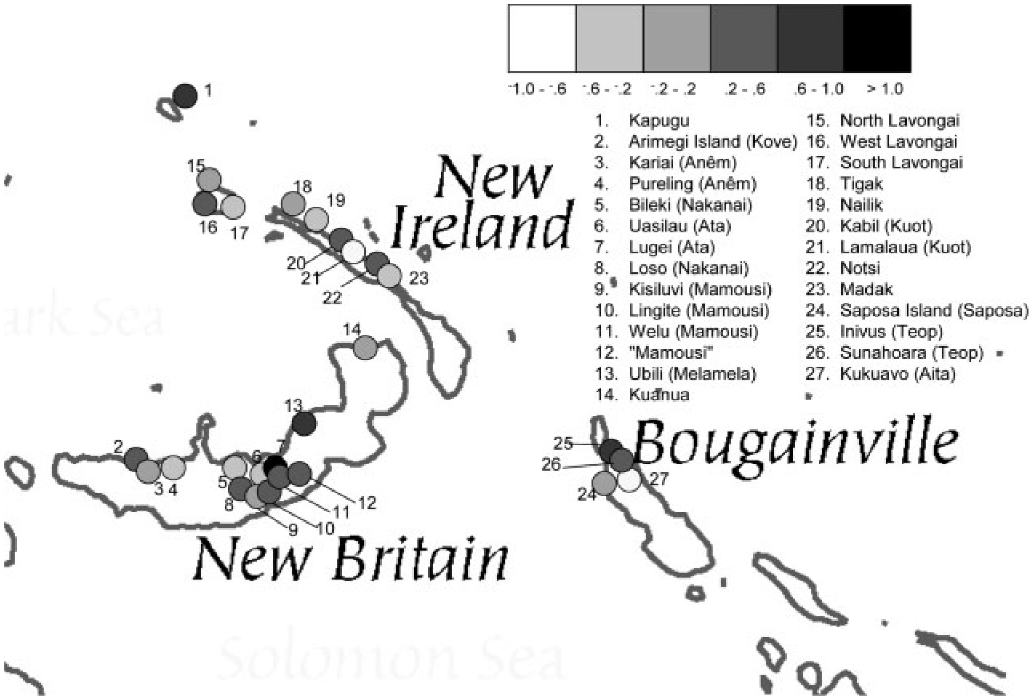

Fig. 4. Sex standardized hair M index for 27 of 28 populations reported in this study (Sepik of New Guinea are not included). Intensity of circle marking each population on map corresponds to pigmentation as measured by M index.

darkly melanized skin in this high UVR region, then hair pigmentation may have been influenced secondarily. While mutations that led to slightly lower levels of melanin in hair pigmentation may not have been selected against in this region, mutations leading to decreased melanin levels in both hair and skin would have been. In this way, variation in hair pigmentation may be generally constrained by selection acting on skin pigmentation. The phenomenon of blondism may be due to a mutation that only affects hair color.

Latitude and longitude

We found no correlation between either skin or hair pigmentation and latitude in this study, which is not surprising, given that this sample covers such a small range of latitudes (9.3°), and most studies stressing the relationship between latitude and pigmentation examined the relationship across a global scale (e.g., Relethford, 1997; Jablonski and Chaplin, 2000). Despite the high levels of variation in skin M index, the relatively dark skin pigmentation of individuals in this study is consistent with expectations for a tropical region, where natural selection may have acted to maintain dark skin as a protection from UV-induced skin damage or folic acid photolysis.

It is important to emphasize that latitude may not be a suitable proxy for UVR in this region, due to effects of cloud cover, humidity, and varying elevations. Thus, the lack of correlation between latitude and skin pigmentation does not necessarily imply a lack of correlation between pigmentation and UVR. With that in mind, however, it is difficult to imagine natural selection exhibiting such fine-tuned regulation of pigmentation at these very localized levels. One useful test of this would be to determine if UVR levels on Bougainville are dramatically elevated relative to elsewhere in the region. If UVR is unusually high there, where pigmentation is darkest, then the case for localized selection of pigmentation phenotype is strengthened.

TABLE 7. Mean M and UVMED values by island

Island	Standardized skin M index	Raw skin M index	UVMED
PNG	−0.552	67.9	275
New Britain	−0.513	67.9	274
Mussau	−0.723	65.5	292
New Hanover	0.433	77.1	289
New Ireland	0.111	74.2	288
Bougainville	1.552	89.8	274

Jablonski and Chaplin (2000) and Chaplin (2004) made use of UVR data collected from the Nimbus-7 satellite (1978–1993) as part of NASA's TOMS project. We examined a smaller TOMS data set for the years 1997–2002 collected by the Earth Probe satellite (http://toms.gsfc.nasa.gov/eptoms/ep_v8.html) to determine mean UV minimum erythemal dose (UVMED) levels across Island Melanesia. UVMED is a measure of the minimum amount of UV exposure required to produce a reddening in the skin of a lightly pigmented individual. While the TOMS data set is the best that is publicly available, one potential problem with using these data in our study region is that TOMS data are reported as UVMED in cells of 1° latitude by 1.25° longitude. We saw that UVMED varied across our region, but that contrary to predictions, Bougainville did not show the highest mean UVMED value (Table 7). Interestingly, the highest UVMED value was observed for the island of Mussau (mean UVMED = 292), which in our study showed the lowest mean skin pigmentation (mean skin M = 65.5). UVMED values for our two other lightly pigmented islands, Papua New Guinea and New Britain, were lower than those observed for New Ireland and New Hanover, but comparable to those of Bougainville.

Hair M index increased slightly but significantly from west to east, while skin M index showed a much stronger increase over the same distance. However, it should be noted that individuals sampled from Bougainville were at the extreme east of our longitudinal distribution and exhibited the darkest skin M index values, making it possible that the Bougainvilleans are responsible for much of this correlation between longitude and skin M index. When Bougainvilleans are excluded from the analysis, longitude is no longer a significant predictor of hair M index, and becomes a weak, although still significant ($R^2 = 0.0225$, $P < 0.0001$), predictor of skin M index.

CONCLUSIONS

Along with a suite of many other genetically controlled phenotypes, pigmentation is a trait that shows remarkable variation and structure within Island Melanesia. Not only was there great variation among islands, but the larger, more rugged islands showed significant internal variation in both skin and hair pigmentation. The geographic patterning of this variation cuts across Austronesian/Papuan boundaries (the possible exception being hair pigmentation in Bougainville), reflecting the complex, but very important, relationship between language, geography, and physical variation in Island Melanesia. In this region, the structure (or pattern) of pigmentation variation echoes the same pattern of variation being elucidated at other loci, suggesting the same overriding effect within this region of demographic determinants (migration, drift, and population history).

The extreme variation exhibited within this sample is not a contradiction to global studies that demonstrated a strong correlation between UVR and skin pigmentation, but it does highlight some unanswered questions and raise some new hypotheses. Because northern Island Melanesia extends from only 1–7° South latitude, it occupies a high UVR environment that should confer an extremely strong selective constraint on skin pigmentation, whatever selective model one favors. In the simplest deterministic model, one might expect everyone there to be as darkly pigmented as Bougainvilleans. That they are not so heavily pigmented, reflecting the strong effects of population dynamics and history, suggests the following alternatives. First, although people have lived in northern Island Melanesia for the past 40,000 years, this may be too short an interval for them to have responded completely to UVR-related selection. How fast UVR-related selection has an effect is very poorly understood. A second hypothesis concerning the variation in this region is that there is a threshold effect with regard to the intensity of UVR-related selection. That is, above a certain "melanin threshold," the force of natural selection on skin pigmentation in high UVR regions may be relatively weak or nonlinear. This hypothesis has some resonance with earlier work relating to critical UVR levels for stimulation of vitamin D_3 synthesis. Such a selective threshold would allow for other factors, such as gene flow, genetic drift, and/or sexual selection, to play a role in shaping localized pigmentation.

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