Reports

Stature, Mortality, and Life History among Indigenous Populations of the Andaman Islands, 1871–1986

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Despite considerable interest in the evolution of small body size, there is little evidence for changes in body size within small-bodied human populations. This study combines anthropometric data from a number of studies of the body size of Andaman Islanders from 1871 to 1986. The colonial history of the Andaman Islands is characterized by high rates of mortality among the indigenous populations. However, long-term conflicts between tribal groups of the Andaman Islands and British and Indian settlers led to some groups being relatively isolated and sheltered from infectious disease and the high rates of mortality that affected other groups. When temporal trends in stature are compared in this context, there is evidence for a reduction in stature among the Great Andamanese who had close contact with the British during the period of highest mortality. Adult stature among the Onge appears to have increased as government involvement diminished following Indian independence. The Jarawa, who had lower rates of mortality throughout the past century, have significantly higher stature than the other groups. These results are interpreted in the context of life-history theory, adaptation, and plasticity. They provide the first long-term diachronic evidence for a relationship between mortality and stature among small-bodied humans.

Positive secular increases in stature have been nearly ubiquitous among human populations globally (Bogin and Keep 1999; Castilho and Lahr 2001; Eveleth and Tanner 1990; Frisancho, Cole, and Klayman 1977; Helmuth 1983; Katzmarzyk and Leonard 1998; Susanne 1985; Tobias 1978; Wolanski 1978). The trend toward increased stature in the past century is commonly interpreted as a correlate of improvements in socioeconomic conditions, diet, and health care (Steckel 1995; Steckel et al. 2002; Susanne 1985). It has been argued that the positive secular trend reveals the genetic potential for the

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attainment of stature before agriculture and urbanization created conditions favoring the reduction of body size (Stini 1975). This argument suggests that larger body size would be characteristic of hunter-gatherers and human populations in general due to past selective pressure.

Several studies have documented negative secular trends in stature (Bogin, Keep, and Edwards 1996; Price 1985; Tobias 1975, 1985; Torretta et al. 1994). These temporal decreases in stature demonstrate that a reduction in body size may be found during periods of particular hardship. Few studies have documented long-term changes in body size among huntergatherers or other nonagricultural societies. When this has been done, researchers have identified neutral or positive secular trends (Comuzzie et al. 1995; Pretty et al. 1998; Tobias 1975). While there is significant evidence for small stature among undernourished populations, poor nutrition may not be the only factor influencing small body size. Differences in growth and age-related stature are likely to have some genetic basis (Martorell 1985).

Small-bodied people (pygmies) are often considered to be a classic example of reduced body size as an adaptation in direct response to selective pressure. Different adaptive mechanisms have been proposed to explain selection for small body size (Diamond 1991) and hormone expressions in different small-bodied groups (Shea and Bailey 1996), such as the fixation of a genetic mutation in African small-bodied people that may change the pattern of normal growth and prevent the adolescent growth spurt (Merimee, Hewlett, and Cavalli-Sforza 1987).

However, previously invoked mechanisms of selection for small body size in human pygmies have recently been questioned by Migliano, Vinicius, and Lahr (2007), who showed that among small-bodied populations there are adaptive advantages associated with attaining larger body sizes. Lifehistory theory explains adult body size as a consequence of a trade-off between time invested in growth and reproduction, both of which are positively associated with fertility (Charnov 2002). High rates of mortality select for earlier reproduction and consequently earlier cessation of growth and smaller body size (Charnov 2002). This pattern is supported by evidence from human pygmies (Migliano, Vinicius, and Lahr 2007), but it may also explain general variation in adult body size among other small-scale societies (Allal et al. 2004; Migliano, Vinicius, and Lahr 2007; Walker et al. 2006).

These studies imply that there is a long-term selective advantage to earlier reproduction, where small body size is a negative "side effect" of this adaptive process. Other studies, however, have emphasized short-term adaptive changes in life-history patterns, such as early reproduction in high-risk environments. Coall and Chisholm (2003) report that under conditions of environmental stress and social risk, girls tend to experience relatively early sexual maturation and fast growth. These changes may happen within one generation, supporting the suggestion that in conditions of uncertainty,

it may be adaptive to reproduce earlier (Coall and Chisholm 2003). This would increase the chances of reproduction before death despite the consequences of small body size. While the pattern described by Coall and Chisholm is a short-term response rather than a long-term selective advantage for earlier reproduction, it shows the existence of a plastic relationship between rates of mortality and age at first reproduction. This relationship may also directly affect adult body size through a trade-off between time invested in growth and age at first reproduction.

To date, there has been insufficient study of the relationships between cultural change, health, mortality, and the pattern of growth among small-bodied human populations. This is primarily due to the paucity of sufficient diachronic anthropometric and demographic data. However, such an analysis would provide valuable evidence of the social, environmental, and biological factors affecting plastic and long-term adaptive changes in stature among small-bodied humans.

We used anthropometric data to track the relationships between social history, mortality, and adult stature among the indigenous populations of the Andaman Islands during the period of colonial occupation from 1871 to 1986. The historic circumstances and relatively late colonization of the Andaman Islands provide a unique opportunity to investigate the relationship between body size and cultural change among small-bodied hunter-gatherers. In this context, we address two primary questions. First, are there body-size differences between tribes who adopted different patterns of social relations with colonial governments? Second, does mortality rate correspond to adult stature among Andaman Islanders? Through consideration of the anthropometric history of Andaman Islanders in this context, this study is the first to test for a diachronic relationship between rates of mortality and stature within populations of small-bodied human foragers.

Geography and Colonial History of the Andaman Islands

The Andaman Islands are a chain of islands situated in the Bay of Bengal, consisting of four primary islands: North Andaman, Middle Andaman, South Andaman, and, approximately 25 miles south, the relatively isolated Little Andaman (fig. 1). Their indigenous inhabitants, small-bodied "Negrito" hunter-gatherers (Cappieri 1974; Radcliffe-Brown 1964), have been the subject of intense interest and debate because of the combination of their phenotypic characteristics and controversial evidence of rare and early genetic lineages among these groups (Endicott et al. 2003; Palanichamy et al. 2006; Thangaraj et al. 2003, 2005). Although there were many tribes, they can be roughly defined geographically and linguistically as the Great Andamanese, the Onge, and the Jarawa. The term "Great Andamanese" describes multiple tribes of the coastal regions of North, Middle, and South Andaman who adopted friendly relations with the British but who maintained distinct dialects. The Onge and Jarawa are both considered to be part

of a single Jarawa linguistic group, with the Onge originally occupying Little Andaman Island and the Jarawa the inland forests of South Andaman Island. The Onge and Jarawa were culturally and linguistically distinct from the Great Andamanese. Despite these distinctions, the tribal groups are generally considered to be morphologically homogenous (Cappieri 1974).

The history of colonialism in the islands and the differing interactions between tribal groups and the colonial settlers are highly relevant. Despite early descriptions of the islands by Chinese explorers and Marco Polo, they are rarely mentioned in historical records because they lie far north of common shipping routes (Chakravarti 1994). The Andamanese occasionally came into contact with Malay, Portuguese, and Dutch sailors from the sixteenth to eighteenth centuries, but they remained hostile toward anyone to land or be shipwrecked in the islands, probably because of their early interactions with Malay traders (Gupta 1994).

The British Colonial Period, 1858-1947

Because of the hostility of the islanders, the British failed to establish a consistent colonial presence before 1858 (Myka 1993). At this time the population of Great Andaman was approximately 6,000 (Portman 1899). Initially, interactions with the British were isolationist, but by the mid-1860s, relations with some of the Great Andamanese tribes were generally friendly as a result of a gift-giving policy (Myka 1993), to the extent that the Great Andamanese populations are often referred to as the "friendly" tribes. These friendly tribes lived in the coastal regions of the three main Andaman islands, but they were enemies of the Jarawa, who lived in the interior forest, and the Onge of Little Andaman Island. The existing hostility between the collective tribes of the Great Andamanese and the Jarawa and Onge dictated the nature of their colonial relations with these groups, as they remained isolationist toward the British after the establishment of the penal

By the late 1860s, some of the Great Andamanese were encouraged to live in government homes established in Port Blair and other outpost locations nearby. The homes were supervised by convicts, who initiated and accelerated the spread of infectious diseases such as influenza and tuberculosis. The British had befriended the majority of tribes by the mid-1870s (Brander 1880), with the notable exception of the Onge and Jarawa. By 1875, syphilis had spread to all friendly tribes. Many who became sick in the residential homes retreated to the forest, where disease spread further. Between 1877 and 1880, a measles epidemic caused very high rates of mortality among the Andamanese populations. By 1900, the population of the Great Andamanese tribes had declined to approximately 600. The population continued to decline to a low of 19 individuals by the 1960s.

The Onge of Little Andaman Island remained isolated from the British until 1885. After contact, the remoteness of Little

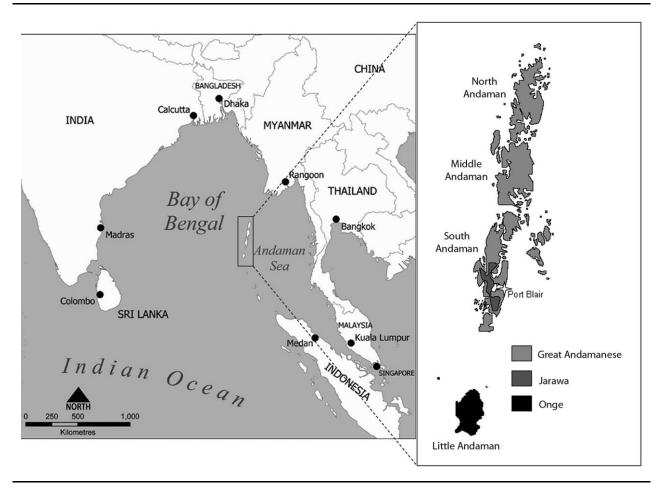


Figure 1. Location of the Andaman Islands and tribal distributions in the mid-1800s.

Andaman Island allowed for less frequent interaction when compared with the Great Andamanese tribes. In 1901, the population of the Onge was approximately 600, and their initial population numbers may not have been much higher. Estimates of Onge demography suggest that the period between 1911 and 1951 was particularly harsh in terms of disease and mortality. During this period there was a 76% decrease in the Onge population size (Kailash 1997).

The British tried to establish friendly relations with the Jarawa but consistently failed. In 1932, a Jarawa territory was officially recognized in the central and western regions of Middle Andaman Island and South Andaman Island. During World War II, the Andaman Islands were occupied and bombed by Japan, and it is thought that many Great Andamanese and some of the Jarawa were suspected of being British informants and were killed by Japanese soldiers (Kailash 1997).

The Period of Indian Independence, 1947-Present

Following independence (1947), the Indian government had little involvement in the Andaman Islands, with a few notable

exceptions. In 1948, it sponsored research to determine the number and health status of the remaining Andaman Islanders (Guha 1952). At this point, the population of Great Andamanese was 23 (Cappieri 1974). The previously isolationist tribes had "been spared the fate of their more 'friendly' kinsmen, as a result of implacable hostility and comparative isolation" (Guha 1952, 1). According to the 1931 Census of India, the total population of "isolationist" tribes was approximately 370 individuals, 250 of which were Onge (Chatterjee 1955), although this probably underestimates the population of Jarawa. Even though the 1948 expedition was unable to obtain accurate population estimates for the Onge, they found members of the group to be in good health, with no signs of sexually transmitted diseases or tuberculosis (Guha 1952).

The Indian Constitution of 1950 initiated increased development, education, and health care for the tribal communities (Myka 1993). Despite this, the government had little effect on the lives of Andaman Islanders until the end of the 1960s, when social planning and exploitation of natural resources became more common. In the early 1970s, the Indian

government began to settle refugees on Little Andaman and soon thereafter opened the islands to forestry, while moving the Onge onto two small reserves (Kailash 1997). In 1968, the Indian government again tried to establish friendly relations with the Jarawa by taking three men captive and later releasing them with gifts. By 1974, they had established sporadic friendly relations with some of the Jarawa people.

A key element of the colonization history of the Andaman Islanders is that Great Andamanese, Onge, and Jarawa established friendly relations with the British and Indian governments at different times. The Great Andamanese tribes participated in the early British programs of commodity exchange, communal housing, and education (Brander 1880). Initially, the Onge and Jarawa groups either were outwardly isolationist toward foreign settlers or simply avoided contact (Man 1883; Radcliffe-Brown 1964). Among these tribes, the Onge were the first to adopt more friendly relations, and they were first studied anthropometrically by von Eickstedt in 1926-1927 (von Eickstedt 1934). The Jarawa of Great Andaman Island remained isolated until the 1970s. One remaining tribe in the Jarawa language family managed to avoid contact with the Indian government until 1991, on remote Sentinel Island (Cavalli-Sforza and Cavalli-Sforza 1995). These historical processes resulted in differences in nutrition, epidemics, and mortality rates among the different tribes and may have had long-term influences on growth and adult body size in these populations. The available evidence for changes in these factors is reviewed below.

Dietary Changes

The subsistence strategy of precolonial Andaman Islanders was based on the exploitation of a variety of marine resources, roots, fruits, and honey from the forest and the communal hunting of wild pigs (Radcliffe-Brown 1964). These sources provided ample provisions with relatively little expenditure of energy as well as the capacity to prepare and store surplus food for later use (Man 1883). After the development of the penal colony and the construction of Andamanese "homes," some of the "friendly" Andamanese were provisioned with cultivated foods. It is known that several hundred acres of forest around Port Blair were cleared in the 1850s for the development of rice agriculture (Sen 1957). There is no evidence to suggest that the Andamanese, whether hunting and gathering or living in the British settlements, suffered from food shortages. Throughout World War II and during the initial decades of Indian independence, the few remaining Great Andamanese lived more or less as they had for decades, while the Onge and Jarawa lived as hunter-gatherers (Sanyal 1976). In the 1970s, however, the diet of the Onge shifted away from hunting and gathering to rice, wheat, coconut, and tortoise (Kailash 1997). Kailash (1997) estimates a caloric intake of 1,862 kcal/day/individual among the Onge in 1969 while living as hunter-gatherers increasing to 2,263 kcal/day in 1989 after the transition to a more agriculturally based diet.

These estimations are low but compatible with the estimated averages for forager populations (Kaplan et al. 2000). There was a reduction in the consumption of specific nutrients such as calcium, iron, vitamin A, and protein following the transition, which caused some health problems (Kailash 1997). Despite this, food shortage does not appear to have been a particular problem, at least for the Onge before 1970, when they shifted away from hunting and gathering. Unfortunately, there are no available records on caloric intake for other Andaman groups or for any of the groups during the previous century. While this limits our ability to confirm whether diets were adequate in different periods, there is no evidence to suggest that they were not.

Mortality, Fertility, and Demographic Changes

Demographic profiles and historical records from the Andaman Islands illustrate a dire picture of disease and health in the Andaman Islands after colonial settlement, particularly among the friendly tribes (table 1). Syphilis and tuberculosis, introduced by convicts of the penal colony, were common among the Great Andamanese, but diarrhoea and malaria also contributed to high rates of mortality (Man 1883). A measles epidemic in 1877 led to a death rate that approached 20% of the total population of Middle and North Andaman (Man 1883). A subsequent syphilis epidemic extended across the same geographic range and affected more than 60% of the population of the Great Andamanese (Man 1883). The extent to which these epidemics reached the Jarawa and Onge is not known, but demographic profiles suggest that the Onge suffered the highest mortality between 1911 and 1951. This im-

Table 1. Population estimates and estimated mortality rates of the various tribal groups in the Andaman Islands, 1858–1989

Year	Populatio	on estim	ates	Estimated deaths (1,000 people/year) ^a				
	Andamanese	Onge	Jarawa ^b	Andamanese	Onge	Jarawa ^b		
1858	$4,800^{\rm b}$			NA	NA	NA		
1867	$3,000^{\rm b}$			19.7	NA	NA		
1901	625	672	585	23.3	NA	NA		
1911	455	631	114	27.2	6.1	80.5		
1921	209	346	231	54.1	45.2	-102.6		
1931	90	250	120	56.9	27.7	48.1		
1951	23	150		74.4	40.0	NA		
1961	19	129	500	17.4	14.0	NA		
1971	19	112	200	0	13.2	60		
1981	19	103	200	0	8.0	0		
1989	28	100	200	-47.4	2.9	0		

Note: Adapted from Myka (1993). NA = not available.

*Estimate of rate of mortality between year and previous census/population estimate, assuming that population change reflects mortality. Actual mortality rates would be higher because they would exclude births. bValues presented are estimates and are likely to be inaccurate, including all of the Jarawa population estimates.

Table 2. Sources of anthropometric data on the Andaman Islanders

				Males		Females		
Researcher	Year ^a	Tribal group	n	Stature (cm)	SD	n	Stature (cm)	SD
Brander	1879	Great Andamanese	15	148.42	4.60	15	137.24	4.11
Man	1883	Great Andamanese	48	149.20		41	140.30	
Molesworth	1893	Great Andamanese	100	148.30		100	139.40	
von Eickstedt	1927	Great Andamanese	10	146.80		22	138.50	
von Eickstedt	1927	Onge	42	148.10		38	138.40	
Guha	1948	Onge	14	148.28	3.76	15	137.86	4.13
Chatterjee	1952	Onge	27	147.79	6.69	23	138.95	3.96
Cipriani	1954	Onge	31	149.46	4.68	20	139.23	3.44
Mitra	1962	Onge	4	151.80		4	140.70	
Sarkar	1985	Jarawa	8	155.03	5.56	8	146.88	5.46
Sarkar	1986	Jarawa	19	152.69	4.72			

[&]quot;Year that anthropometric data were recorded (not always the same as the year they were published).

plies that they also suffered from diseases spread at the colony, but their relative isolation and hostility buffered some of the severity of these illnesses during the early colonial period.

In a population suffering extreme demographic transitions like the Andamanese, fertility is likely to be affected. One reason to expect a decrease in fertility is the difficulty in finding partners when the breeding population is reduced; this also increases the levels of endogamy, which is likely to further affect fertility levels (Headland 1987). The problem of finding a partner can be illustrated by the incompatible ages of spouses: "A significant proportion of Andamanese and Onge are reported to be barren because of the age differences of their spouses who have crossed the reproductive span" (Kailash 1997, 399). Further complications resulted from the epidemic of syphilis (Mukerjee 2003) and the fact that the Andamanese are monogamous and marriages do not take place with near consanguines (De 1970).

Although reported fertility rates are low among the Andaman Islanders (Great Andamanese = 3.5, Onge = 4.4), they are not particularly different from those observed in other regions of India (3.75 in 1971; Malhotra 1989). In 1893, the total number of births reported per Great Andamanese woman 45 years old or older was 3.2 (W. S. Molesworth, unpublished monograph, 1893; described in Cappieri 1967). Thus, the available evidence suggests that fertility among the Andaman Islanders may have been relatively stable over the past century without declines associated with specific demographic changes. This suggests that low fertility rates were not the primary cause of population decrease among indigenous Andaman Islanders.

Increased mortality rates, on the other hand, seem to have been the main cause of depopulation among Andamanese groups. There are no systematic records of rates of mortality per year; however, multiple indicators demonstrate extreme levels of mortality in different periods of contact. Homfrey (described in Cappieri 1953) noted that in 1866 at Port Mouat, 15 births were registered among the Andamanese population, and not one infant survived. W. S. Molesworth (un-

published monograph, 1893) later recorded 149 births among 100 Great Andamanese women, and only 26 children survived (a mortality rate of 82.6%). Malhotra (1989) reported an infant mortality rate of 60% among the Onge and high mortality rates among young adults (between 20 and 34 years old). A further 28.6% of Great Andamanese and 57.6% of Onge died before achieving reproductive age. A similar mortality profile has also been found in other small-bodied and Negrito groups in Africa and the Philippines (Migliano, Vinicius, and Lahr 2007). Given that there is almost no outgroup migration and that fertility rates appear to have been relatively stable, we use rates of population decrease as a proxy for mortality rates in this study.

The mortality rates among Andamanese Negritos are as high as those observed in other small-bodied groups and were probably the primary cause of depopulation. Because variation in adult body size can be followed through the nineteenth and twentieth centuries, the anthropometric history of these groups provides a rare opportunity to test the relationship between mortality rates and body size among small-bodied hunter-gatherers by considering adaptation and plasticity in life-history strategies. In the context of the colonial history of the Andaman Islands, we consider whether the differing patterns of colonial relations between the Great Andamanese, the Onge, and the Jarawa—and their respective influences on health—influenced body size in the Andamanese. When diachronic and spatial trends in stature are placed in the context of recent evidence for a relationship between mortality and stature in human populations, do patterns of mortality among the tribes of the Andaman Islands correspond with stature?

Material

Anthropometric data used in this study were derived from 11 governmental and anthropological expeditions between 1879 and 1986 (table 2), measuring a total of 604 individuals (n = 604; M = 318, F = 286). Data were first collected by E. S. Brander (1880) in 1879, 21 years after the British coloni-

zation of the island, while further measurements of the Great Andamanese were published by Man (1878, 1883, 1885) and W. S. Molesworth (unpublished monograph, 1893). In 1926–1927, von Eickstedt (1928, 1934) measured members of friendly tribes of Great Andaman and was the first to measure the stature of the Onge (fig. 2), followed by Guha (1952), Chatterjee (1955), Mitra (in 1962; Cappieri 1974), and Cipriani (1966). In 1985–1986, Sarkar (1989) conducted the first known anthropometric research among the Jarawa.

There are a number of limitations caused by the use of aggregate and historical data sets of this nature. Primarily, individual data are available for only a few studies, limiting the possible statistical analyses. Second, the collection of census and anthropometric data is complicated at best, and errors may have been introduced during the collection of data from populations with differing relations to the government or by different researchers. Although unlikely, we cannot exclude the possibility that in some of the cases, the same individual may have been measured by different researchers. Finally, small sample sizes limit the utility and reliability of regression analyses.

Despite these limitations, the data provided by these studies represent the only long-term diachronic anthropometric data of a small-bodied population in existence. The relatively late colonial occupation of the islands and the immediate interest in the anthropometric characteristics of their inhabitants by the colonists provide rare data collected shortly after colonization. In addition, the historic spacing of these anthropometric studies provides an opportunity to investigate the relationship between stature, health, and colonialism among hunter-gatherers. In the context of the history of social relations between the Andaman Islanders and the British and Indian governments, the available data also allow us to test for a relationship between the pattern of body-size adaptation and the population history of different tribes. In these contexts, the limitations of these data are frustrating; however, they provide the only known data set with which to test for morphological change of hunter-gatherers in the face of very high rates of mortality immediately following colonial settlement.

While the number of studies is small, and perhaps prohibitively so in the case of Great Andamanese body size, least squares regression was applied to sample-size-weighted population means to provide a basic heuristic indicator of diachronic changes in stature. Regressions were performed for the combined sample, ranging from 1879 to 1986 (n=604), and the subsets of the data that represented tribes who adopted either "friendly" or "isolationist" relations with the British and Indian governments. Locally weighted scatterplot smoothing (LOWESS; Trexler and Travis 1993) was used in

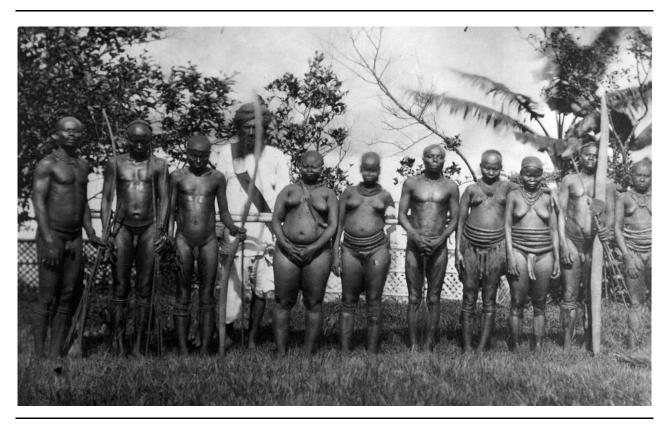


Figure 2. Great Andamanese, late nineteenth century. From the photographic collection of Maurice V. Portman, courtesy of the Natural History Museum, London.

bivariate scatterplots to explore temporal trends in stature. Mortality rates were estimated from the rate of population change per year between two subsequent census/population estimates, assuming that population change reflects mortality. This produces conservative estimates that exclude births, and as such, they underestimate actual mortality rates. These estimates are used to test for a relationship between mortality and stature.

Results

If we compare stature of the Andaman Islanders with the study date for the combined samples, there appears to be a very modest increase in stature among both men and women (table 3), despite fluctuations throughout the past century. The slope of the female data (0.0104) between 1879 and 1985 suggests that there was a slight nonsignificant increase in adult stature (ca. 1 cm/100 years; $r^2 = 0.041$, P = .577). A comparable analysis of male stature versus date identifies a stronger positive secular trend, with male stature increasing on average 2.4 cm/100 years. Although the correlation for this analysis remains low ($r^2 = 0.280$), the regression is nonsignificant at the 95% confidence level (P = .094). These results suggest a broad pattern of stability in stature through time; however, they are potentially misleading because of the combination of different tribal groups.

By subdividing into Great Andamanese "friendly" and Onge and Jarawa "isolationist" tribal groups, the results correspond with the inflections in the combined data set more closely. Weighted regressions of sample means illustrate a decrease in stature (-4.7 cm/100 years) among males of the tribes with friendly relations with the British between 1879 (Brander 1880) and 1927 (von Eickstedt 1928). While nonsignificant and tenuous because of the number of samples, the morphological trend is suggestive of a decrease in stature among friendly tribes in the early colonial period and following the period of most severe mortality.

The earliest study of the Onge (1927) recorded male stat-

ures that were similar to those of the Great Andamanese measured on the same expedition and those of the Onge measured by Guha in 1948. Subsequent studies recorded higher values, which increased until the most recent study in 1962. Statures reported by Sarkar for the Jarawa in 1985-1986 are the highest values recorded for the Andaman Islanders. Overall, if we consider stature among the Onge and Jarawa collectively, as tribes who remained isolationist toward the British, there is an increase in stature following the initial study in 1948 (Guha 1952) that equates to a rate of approximately 8.9 cm/100 years (slope = 0.089; $r^2 = 0.717$, P =.016). However, this comparison is heavily influenced by recent body size data of the Jarawa and does not consider potential differences in body size between the Jarawa and Onge. Considering only the Onge males produces a nonsignificant regression (P = .389) with a modest correlation between the variables ($r^2 = 0.252$) and a considerably lower slope of 0.036, equivalent to a 3.6 cm/100 year increase in stature within this group (fig. 3).

The Great Andamanese females show a relative stability in stature among the friendly Great Andamanese tribes (fig. 4), with only a modest decrease during this period (-1.8 cm/ 100 years; table 3). Statures of Onge women recorded by Guha in 1948 were among the lowest recorded and were lower than the mean stature of Onge women measured by von Eickstedt (1934). Subsequent larger anthropometric surveys by Chatterjee (1955) and Cipriani (1966) recorded higher statures for the Onge women in 1952 and 1954. The small study of eight Onge by Mitra in 1962 (Cappieri 1974) reported higher statures than any of the previous studies and contributes to a modest but nonsignificant positive relationship ($r^2 = 0.329$, P = .312) between Onge stature and the date of study. Although there are limitations to this comparison based on von Eickstedt's and Brander's data, if we accept these measurements as being indicative of mean statures at this time, the results suggest an increase in women's stature between 1948 and 1962, a result that reaches statistical significance in this

Table 3. Regression coefficients and rates of stature change, weighted sample means

Tribes and sex	Temporal range	Data sets	Total n	Slope	Intercept	r^2	P	Rate of change (cm/100 years)
All:								_
Female	1879-1985	10	286	.010	120.49	.036	.598	3.6
Male	1879-1986	11	318	.024	102.29	.280	.094	2.4
Great Andamanese:								
Female	1879-1927	4	178	018	173.15	.087	.706	-1.8
Male	1879-1927	4	173	047	4,323.55	.767	.124	-4.7
Onge:								
Female	1927-1962	5	100	.028	84.83	.329	.312	2.8
Male	1927-1962	5	118	.036	79.18	.252	.389	3.6
Onge and Jarawa:								
Female	1927-1985	6	108	.103	-61.53	.582	.078	10.3
Male	1927-1986	7	145	.089	-24.82	.717	.016*	8.9

^{*}Statistically significant regression ($P \le .05$).

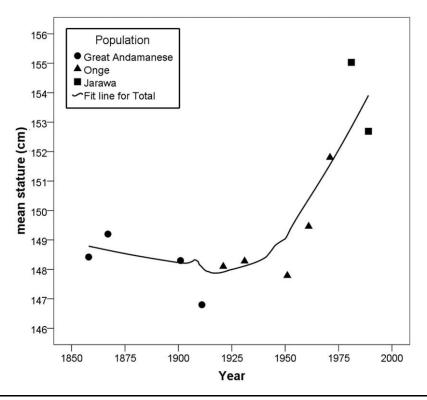


Figure 3. Mean statures for male Andaman Islanders versus time by population and with locally weighted scatterplot smoothing (LOWESS; 11 samples, total n=318). Points are derived from the studies described in table 2. LOWESS lines are based on Epanechnikov line fitting of 75% of points.

interval. The mean stature of eight Jarawa women measured in 1985 (Sarkar 1989) is the highest value recorded. While the relationship of statures across this interval suggests a reasonable positive secular trend in stature, the inclusion of the Jarawa data is clearly driving the results. At present, there is insufficient data to determine whether Jarawa stature has changed through time or whether this study is identifying previously undocumented morphological differences between groups. It is possible that larger body size is a general morphological characteristic of the Jarawa, due to either genetic differences or their relative isolation from diseases associated with colonial relations. ANCOVA was used with an interaction effect to test for homogeneity of regression slopes. The results indicate that there are significant differences in temporal trends in stature between the tribal groups among both the males (P = .019) and the females (P = .006). While the evidence for secular trends based on regression analyses can be considered only tentative because of the limitations of the data available, there are significant differences in stature between tribal groups.

To test whether differences in mortality can be correlated with differences in stature, population size estimates were used to estimate mortality rates (table 1) and were compared with statures throughout the colonial period, using cubic regression. The results show a strong relationship between stature and mortality in the previous decade (or since the preceding population estimate or census). Figure 5 illustrates that higher mortality rates are clearly associated with lower mean statures. The relationship between stature and mortality is strong and statistically significant among males ($r^2 = 0.892$, P = .001) and females ($r^2 = 0.859$, P = .006). These results provide reasonable evidence that despite diachronic trends and tribal differences in stature, variation in body size among the Andaman Islanders is related to differences in mortality.

Discussion

The comparison of anthropometric data among indigenous Andaman Islanders suggests that there was a general reduction in stature among the Great Andamanese tribes that adopted friendly relations with the British early in the colonial history of the islands. This trend is associated with high rates of mortality from infectious diseases spread through the colonial settlements into the tribal regions throughout Middle Andaman Island and North Andaman Island. The general decline in stature during this period corresponds with a period of sustained high rates of mortality. Despite inherent limitations in the current data set, it provides the best available evidence

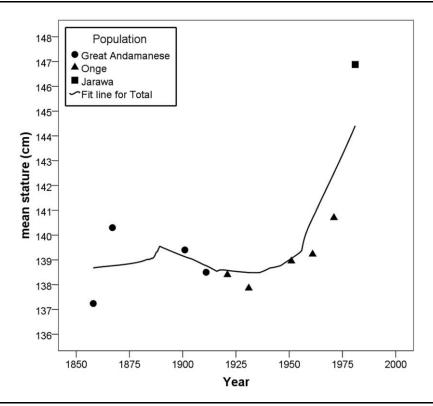


Figure 4. Mean statures for female Andaman Islanders versus time by population and with locally weighted scatterplot smoothing (LOWESS; 10 samples, total n=286). Points are derived from the studies described in table 2. LOWESS lines are based on Epanechnikov line fitting of 75% of points.

for diachronic change in physique among small-bodied hunter-gatherers, and it is the first tentative evidence of a negative secular trend among these groups.

The tribes who remained isolationist throughout the early colonial period were more successful at avoiding infectious disease. The population of these tribes did not collapse to the extent of the friendly tribes, although the estimated population of Onge decreased dramatically between 1901 and 1951. The first Onge anthropometric data (1927) was collected in the middle of a 40-year period of high mortality. At this time, mean statures of the Onge were comparable with the recorded statures of the friendly tribes during the height of their epidemics. Over the following 2 decades, consistently higher adult statures were recorded for the Onge. This suggests that there was a rapid period of rebound in growth during the early independence period, when government interaction was at a minimum and the Onge lived as hunter-gatherers. The Onge were undoubtedly affected by disease and elevated mortality as a result of the British attempts to establish relations. The extent of morbidity and mortality in the early British colonial period before 1901 is poorly known, but the anthropometric history of the Onge suggests that health and mortality improved when the policy of colonization was relaxed.

The only published measurements of the Jarawa tribes are the highest recorded for both male and female indigenous Andaman Islanders. This may be the result of the relative isolation and hostility of the Jarawa tribes toward both the colonial settlers and the friendly Andamanese tribes. Although earlier demographic estimates for the Jarawa suggest that the population was more stable than the Onge or the Great Andamanese throughout the colonial history of the Islands, there is no temporal depth to the Jarawa anthropometric data. Their tall stature in the 1980s combined with the evidence for greater demographic stability suggests that they remained relatively healthy throughout the colonial period. It may be the case that the stature of the Jarawa represents a closer approximation of the genetic potential for growth among the other Andamanese tribes and that all other anthropometric data reflect in part the difficult history of the Andamanese people. Overall, the rates of decline in stature suggested by the Andaman Islander data appear to be among the highest rates of change in stature observed in recent human populations (Eveleth and Tanner 1990).

The reasons for negative secular changes for the Great Andamanese cannot be explored in detail with the available data set. The body size of these populations may have been influenced by different, nonexclusive factors. The most likely al-

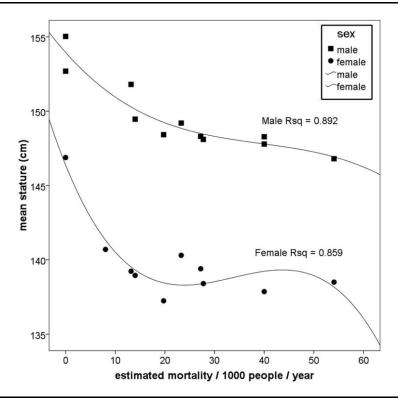


Figure 5. Estimated mortality rates and stature in the Andaman Islands by sex and using weighted cubic regression (21 samples, total n = 604).

ternate explanation would be poor nutrition related to dietary changes after contact, where there would be a trade-off between growth and metabolic maintenance. However, there is no evidence of significant and permanent changes in diet until the 1970s (Kailash 1997), long after the Andamanese had gone through a reduction in body size. Another possibility is that higher incidences of disease lead to a readjustment of energetic investment as a consequence of adaptive trade-off between immunological repair and both growth and body maintenance, negatively affecting adult body size (Bogin, Varela-Silva, and Rios 2007). Both poor nutrition and slow growth lead to late sexual maturation and late reproduction, which results in a trade-off between growth and reproduction (Stearns 1992). Although there is no known data of age at first reproduction among the Andamanese, an interesting report suggests that there is strong pressure for early reproduction. Sudarsen (1994) showed that in 1988, all Onge girls 11 years old or older were married, and the only three Great Andamanese women older than 14 years were married as well. This is weak evidence for early reproduction; however, the Andamanese seem to follow the pattern described for other small-bodied groups in which high mortality rates and depopulation lead to pressure for early reproduction, which may indirectly influence growth and adult body size.

In the case of other small-bodied and Negrito groups, the relationship between mortality, reproduction, and body size has been shown to be adaptive, shaped by natural selection for earlier reproduction, consequently leading to small body size (Migliano, Vinicius, and Lahr 2007). In this study, a reduction in body size is observed among the Andaman Islanders over a span of 48 years in the early colonial period. Increased mortality rates may have also increased selective pressures for early reproduction, especially on an island where body size reduction can happen rapidly (Millien 2006). However, it is unlikely that genetic (adaptive) changes would be manifest in such a short period, especially in such a small and declining population in which the strength of selective pressures is likely overcome by drift (Hawks et al. 2007; Kimura 1983).

It is possible that high mortality rates shaped life-history strategies and consequently body size of the Andamanese Negritos before contact, given that Andamanese adult body size has always been in the range of the African Pygmies and other Negrito references for historical body size. With the increased mortality rates after contact, reduction in body size may have been intensified by plastic mechanisms such those proposed by Coall and Chisholm (2003), where stressful environments and high risks of mortality lead to earlier reproduction.

The secular association between increased mortality levels and decreased body size in the Andamanese has two important implications for the evolution of diversity in human body size. First, both genetic adaptation and plastic responses to high rates of mortality lead to a reduction in body size (this is expected because plasticity is also adaptive and should increase the capacity of a fast response to the same environmental stresses). Second, small-bodied populations who are already at the extreme of one adaptive strategy (at the fast extreme of the life-history continuum) are still able to respond plastically to even higher mortality pressures, reducing body size even further. However, this does not seem to be a sustainable adaptive strategy, given that these populations were driven close to extinction.

Conclusions

Long-term variation in mortality, related to tribal differences in relations with the British and Indian settlers, appears to explain much of the variability in stature found among the indigenous Andaman Islanders. This colonial relationship led to differences in mortality among these tribes, which appears to have been a fundamental determinant of variation in body size. This interpretation is supported by evidence for a reduction in stature during the period of highest mortality among the Great Andamanese who had close relations with the British following their settlement in the 1850s. In contrast, Onge stature appears to have increased as government involvement in Little Andaman Island diminished following Indian independence in 1947. The Jarawa, who maintained isolationist relations with both the British and the Indian governments until recently and who are presumed to have had lower rates of mortality throughout the past century, have significantly higher stature than the other groups. The trends in stature noted among these groups follow life-history predictions, where high mortality rates lead to smaller body size; however, causation cannot be assumed here, and different factors could be responsible for this correlation, such as a combination of plastic and/or genetic adaptation to high mortality rates.

The available historical records in the Andaman Islands provide a rare diachronic sequence of human physique and demography during a colonial transition. Cultural change among the friendly tribes was abrupt and corresponded with very high rates of mortality, on the basis of which stature appears to vary. There is evidence of (a) reduced stature among tribal groups who maintained consistent and friendly relations with British settlers and (b) a correlation between stature and rates of mortality among the populations of the Andaman Islands. These results suggest that some aspects of body size among small-bodied populations may be driven by patterns of mortality related to relationships with neighboring populations. The observation of diachronic size reduction in relation to mortality among small-bodied humans may help us to understand the diversification of human body size and the process of island dwarfism (Foster 1964) in humans (Berger et al. 2008) and other hominins, such as Homo floresiensis (Brown et al. 2004), but it also informs us about possible interactions between plasticity and adaptation in the evolution of human phenotypic diversity.

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