

CHAPTER 3

LITERATURE REVIEW

3.1 INTRODUCTION

The aim of this chapter is to provide a research context for the analysis to follow. The first section will review the work of Joseph Birdsell and how his work influenced Australian palaeoanthropology and more specifically, this thesis. The next section will summarise the literature on ecogeographic rules, beginning with the historical background to these studies and then reviewing the observational and experimental evidence of the effects of environmental factors, in particular climate, on the morphology of animals and humans. Studies regarding body size and proportions are dealt with first followed by those on the head and face. The final part of this chapter will review how such research has influenced arguments about the origins of modern humans and other aspects of hominid evolution.

3.2 JOSEPH B. BIRDSELL

3.2.1 Expeditions and Research

As the author did not collect any of the materials to be used in this research it is appropriate to provide a context for these data. This is necessary because the nature and structure of the database, as well as its strengths and weaknesses can, in part, be explained by who collected the data, and why they were collected. A more detailed discussion of the actual data can be found in Chapter 4.

The vast majority of the data to be used in this thesis were recorded by Joseph Birdsell during two expeditions to Australia in the 1930s and 1950s. Birdsell first came to Australia in 1938 whilst a graduate student at Harvard University. This first expedition was a collaborative project between Harvard and Adelaide Universities and the South Australian Museum and took place over 14 months between 1938 and 1939. By the time of the second expedition (late 1952 to early 1954) Birdsell was employed at U.C.L.A. and, once again cooperating with Adelaide University and the South Australian Museum, spent a longer period of time adding to his database (Birdsell 1941, 1949, 1967, 1977, 1993; Tindale & Birdsell 1941). His major collaborator on both expeditions was Norman Tindale of the South Australian Museum whose influence was to significantly alter the course of Birdsell's research work.

The 1938-39 expedition was part of a project designed by Earnest Hooton on race

mixture in Australia (Birdsell 1941, 1967). Birdsell was to record that he "arrived in Australia convinced that the Aborigines represented a homogeneous population with no significant regional variation" (Birdsell 1967: 100). He related that his initial intention was to measure "hybrids" (Australoid, Caucasian crosses), and only collect data on full-blood (unmixed) subjects as a check sample (Birdsell 1941: i-ii). The aim of the research dictated the observations and measurements taken. These included standard anthropometric measurements of the body, head and face, as well as qualitative assessments on traits such as pigmentation, the shape and relative size of various body, facial and dental features, and also the typing of the blood antigens systems ABO and MNSs. However, Birdsell went on to record that after a short period of field-work it became apparent that the regional differences among Aborigines were:

"probably of ethnic rather than local magnitude, and efforts were made to obtain, as a secondary purpose of the project, as complete a sample of full-blooded natives as was compatible with the major study of race mixture" (Birdsell, 1941: ii).

He concluded from his observations, combined with those of the better travelled Tindale, that the indigenous peoples of Australia were not homogeneous and that there was a great deal of previously unrecognised and unexplained regional variation. He felt that the origin of this regional variation was a far better story to tell and this became the focus of his PhD dissertation, "The Trihybrid Origins of the Australian Aborigine" submitted in 1941. The project on race mixture was never completed.

His expedition of 1952 to 1954 was motivated by very different research aims. His shift from Harvard to U.C.L.A. also saw a paradigm shift in his thinking about human evolution. His interests had progressed from what could be termed the Old Physical Anthropology concerned with racial typology to the New Physical Anthropology concerned with evolutionary genetics and stochastic processes. However, it is interesting to note that despite this radical departure from his academic roots at Harvard, he maintained his belief in the tripartite ethnic origin of the Aborigines until his death in 1994 (see Birdsell 1993).

In Australia he is possibly best remembered for his work on Aboriginal origins, along with his articles on Aboriginal ecology, land use, demography and genetics (Birdsell 1941, 1949, 1950, 1953, 1957, 1958, 1967, 1970, 1971, 1972, 1973, 1976, 1977, 1978, 1979, 1987, 1993; Birdsell, *et al.* 1979).

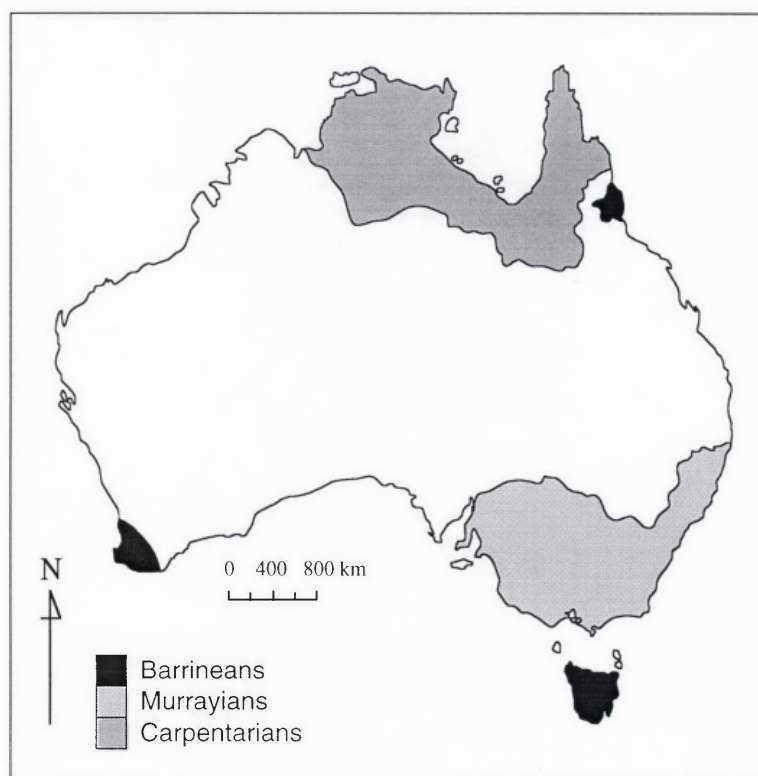


Figure 3.1: Distribution of Birdsell's three founder groups. Unshaded areas represent populations descended from a mix of the founder groups, adapted from Birdsell, 1967:110.

In his thesis and various publications (Birdsell 1941, 1949, 1967, 1993; Tindale & Birdsell 1941), he argued that there were three major migrations into Australia. The first migrant group he originally designated "Tasmanoid" because of their supposed likeness to the indigenous inhabitants of that island. They were later renamed "Barrineans" after Lake Barrine on the Atherton Tablelands of far North Queensland, which he identified as the centre of their second major area of distribution. This first wave he likened to the Oceanic Negritos (Birdsell 1941: 231), arguing that they represented the earliest substratum of *Homo sapiens* in the Asia-Pacific region: a theory that has a long history (see Brown 1997). Negrito was the term originally given to the Pygmy peoples of Central and Western Africa. The populations known as Oceanic Negrito were found in isolated pockets of rainforest in Southeast Asia and include the Aeta of the Philippines, the Semang of Malaysia and the indigenous people of the Andaman Islands. Also sometimes included with this group are New Guinea Highlanders. These groups shared in common dark skin, small stature, frizzy or peppercorn hair, and infantile facial features. In the Andamanese Negritos the women also exhibited steatopygia, a feature not of African Pygmies but of Koi-San peoples of Southern Africa. The Tasmanoids or Barrineans certainly shared some of these features including dark skin, small stature and scant body

hair, however their head-hair, according to Birdsell, was either crisp and tightly helically curled, or had a deep wave, but did not display the frizzy or peppercorn hair of the Negrito (Birdsell 1993: 216-222). Their facial features were somewhat more infantile than other Aboriginal groups but this may simply be the result of allometry. Birdsell described their body proportions as:

“more or less normal, but the distal segments of the limbs are elongated relative to the proximal portions. Both types of prognathism [facial and alveolar] are common, and the teeth are relatively small for an Australian group, and differ from the other types in the cusp pattern of the lower molars” (Birdsell 1941: 229).

Birdsell argued that these first immigrants to Australia were pushed aside into refuge areas in North Queensland and Tasmania by the next wave of immigrants whom he called the Murrians (later Murrayians). These were described as a people of light unexposed skin colour, with a low wave to their hair and an increased frequency of baldness, but with extremely abundant body hair. Their body build was short, but more lateral and stocky, and they were prone to obesity in adulthood. Their body proportions are described as:

“relatively normal for Australians, and although the lower segments of the limbs are relatively longer than usual among most peoples, it can be said that this ethnic group approximate White standards metrically and indicially much more closely than do either of the two other types. Head length is very great, the breadth is moderate, and the height is low. The forehead and jaw breadths are great for Australians, and the large faces seem to dominate the vault. The nose is broad and coarse, but the nasal relief is rather high. Prognathism is less common among these people than the other Australians...” (Birdsell 1941: 229-230).

He felt that the Murrayians had a rough-hewn Caucasian appearance and argued that this linked them with the Ainu of Japan, a group also identified at the time as "archaic Caucasian" (Birdsell 1941: 231).

The third and final wave of immigrants Birdsell identified as "Carpentarians", again because of the geographic location of the group. They were typified as being of tall stature, very dark-skinned, with head hair of low wave and no crispness, and with very little body hair. Their body proportions were:

“extremely linear, with a relatively short trunk, very elongated lower limb segments, and meagerly developed calf musculature. ... Despite the tall stature, the head is only moderately long, and very narrow. The height is rather low absolutely, but high relative to the two other dimensions. Faces are short, but rather broad. The nose is in low relief, and

coarse in its modelling. ... Both alveolar and facial prognathism are greatly developed, and the teeth are large, although not quite so extreme as among the Murrians” (Birdsell 1941: 230).

These people he likened to the Veda of Sri Lanka (Birdsell 1941: 231-232).

He theorised, admittedly on slim evidence, that the:

“Negritic peoples came through Indonesia into Melanesia and Australia in Late Pleistocene times, subsequent to the extinction of *Homo soloensis* in Java, and that they populated the entire Australian continent. At some later date, but prior to the extinction of the giant marsupials, the Murrian wave of peoples reached Australia, and almost completely absorbed the previous Negritic element” (Birdsell 1941: 232).

The Murrayians were identified as making up the majority of the Aboriginal population at contact, with the negrito-type peoples to be found in their purest form in refuge areas such as Tasmania, the Cairns rainforest, the "extreme" southwest of Western Australia, the eastern coastal strip and on Mellville and Bathurst Islands to the north, but that traces of this population substratum could be found all over Australia (Birdsell 1941: 214). The Carpentarians, Birdsell explained, were recent migrants and had not spread their influence very far at the time of European contact (Birdsell 1941: 232) (see Figure 3.1).

Birdsell's tri-hybrid theory was taught in Australian courses on Aboriginal Prehistory, but it was given little credence by scholars working in Australia. It is probable that his theory had more currency in the United States where Birdsell taught and published several influential undergraduate texts on physical anthropology, than it did in Australia. The major reason for the lack of support in Australia is because of the absence of fossil, archaeological, linguistic or genetic evidence to support three large-scale migrations (see White & O'Connell 1982; Yengoyan 1995: 29; Brown 1997; Mulvaney & Kamminga 1999: 153-155).

This is not to disparage or discount his work, which is outstanding in Australian physical anthropology for its scope. No other single anthropologist working in Australia amassed the spatial breadth of data on living Aboriginal people that Birdsell succeeded in collecting. Among his most lasting contributions were his meticulous mapping of the extent of water barriers during ice-age low sea levels and the possible migration routes into Australia, as well as his contributions to the understanding of human ecology and demography in Aboriginal Australia.

3.2.2 Birdsell and Ecogeographic Rules

As mentioned above, Birdsell's academic roots lay in the paradigms of the Old Physical Anthropology and racial typology, although he was soon to move beyond these. Early in his career he collaborated in the much-cited book "Races... A study of the problems of race

formation in Man" with Carlton Coon and Stanley Garn (Coon, Garn, & Birdsell 1950), a work that Pat Shipman has called "one of the first, brilliant attempts to take an ecological and evolutionary view of modern humans" (Shipman 1994: 186). The thesis of the book, based on a series of lectures, was that much of the variation evident in modern humans was the result of long-term adaptation to environment: be it the heat and sun of Africa, the cold of northern Asia, or the cold, damp and fog of northwest Europe. Birdsell, however, influenced by the new synthetic theory of evolution came to understand that natural selection was not the only evolutionary force. In particular he was influenced by, and was to become a fervent admirer of, Sewell Wright's thesis of stochastic processes in evolution (Wright 1922, 1931, 1939, 1978) and this was to significantly alter the way he analysed the material he had collected in Australia.

In fact, Birdsell was later to repudiate Coon's selection/adaptation theory of racial origins (or modern human biogeography), calling it "easy evolution" which ignored "the real variabilities of the population concerned and the complexities of evolutionary processes" (Birdsell 1967: 108). He argued in his 1967 paper that the very extent of the distribution of Murrayian type, ranging as it did from the cooler south, into the hot-arid regions of the southwest and up the east coast into the tropics, denied the possibility that the "the pattern of regional differentiation did not favor selective changes as the sole, or even the primary, cause of the observed differences between the Murrayians and Carpentarians" (Birdsell 1967: 146). He conceded that "local adaptive changes were no doubt present" (Birdsell 1993: 450) but that the two main sources of geographic variation in Australia were firstly ethnic origin (gene flow) and overlaying this the stochastic processes of drift, bottleneck and founder effect.

Table 3.1: Environmental variables in four test regions, after Birdsell, 1993: 450, Table F-6.

Variable	Southeast (B10; B11)	Southwest (B1; B2)	Northwest Kitja (T5)	Northeast Lower Cape York (B-23)
1. Extreme temperatures (25 years)	107-118°F	105-115°F	110-115°F	105-112°F
2. No. days over 100°F (per year)	0-40	0-20	60-100	20-60
3. Hours of sunshine (per year)	2250-3250	2000-3000	3250-3500	2750-3250
4. Net daily radiation: January (cal cm ⁻¹ day ⁻¹)	290-330	290-330	330-335	305-315
5. Net daily radiation: July (cal cm ⁻¹ day ⁻¹)	15-45	40-60	140-150	130-170
6. Mean annual temperature	50-65°F	50-65°F	Above 80°F	Above 80°F
7. Mean January temperature	65-80°F	65-75°F	85-90°F	80-85°F
8. Mean July temperature	40-50°F	45-55°F	65-70°F	70-75°F
9. No. frost free days (per year)	150-365	100-365	300-365	365
10. Mean annual rainfall (in)	12-63	12-63	24-31	31-47
11. Mean annual evapotranspiration (in)	5-40	10-30	20-30	30-40
12. Growing season (months)	6-11	7-9	2-3	2-4
13. Vegetation	Variable	Variable	Open forest	Open forest

Table 3. 2: Biological variables in four test regions, after Birdsell, 1993: 451, Table F-7.

Variable	Southeast (B10; B11) n = 40-44	Southwest (B1; B2) n = 39-41	Northwest Kitja (T5) n = 35-37	Northeast Lower Cape York (B-23) n = 23-26
1. Skin colour (to scale values)	2.6	3.6	4.9	4.2
2. Median age of greying (years)	36.9	36.9	30.3	25.6
3. Baldness (percent over 50 years)	35-40	10-15	10-15	5-10
4. Beard abundance (to scale)	4.4	3.6	2.9	2.5
5. Weight (lbs)	142	129.3	126.9	129.7
6. Stature (cm)	164.7	163.5	170.5	129.7
7. Relative sitting height (percent)	51.3	50.4	50.9	50.5
8. Relative shoulder breadth(percent)	23	22.5	21.2	21.8
9. Humeral-sitting height (percent)	39.6	40.3	39.3	39.5
10. Radial-sitting height (percent)	31.3	31.8	31.4	32.2
11. Femoral-sitting height (percent)	53.7	55.2	55	54.9
12. Tibial-sitting height (percent)	44.6	47.1	46.7	47
13.Calf-tibial (percent)	87.1	81.3	75.8	79.6
14. Age (years)*	53	45	39	46

(*Age has been included here to highlight the age differences between his sample groups.)

In his 1993 monograph he conducted a small-scale analysis to prove his point. He selected four sample areas, the Southwest, Southeast, Northwest and Northeast Lower Cape York, each pair of which had similar climates but were widely separated in space (see Table 3.1, adapted from Table F-6 Birdsell 1993: 450). He then compared the various anthropometric measurements and phenotypic traits of groups from these regions (see Table 3.2, adapted from Table F-7 Birdsell 1993: 451).

He concluded that despite the Southwest having a climate roughly similar to that of the Southeast the people he measured had more in common with the populations in the north (Carpentarians) (Birdsell 1993: 450-451). From this he deduced that ethnic origin was responsible for this pattern of variation not natural selection. Yet in an earlier work he ascribed the morphological differences between the ethnic groups that migrated into Australia to have "evolved as a consequence of regionally determined adaptive processes" (Birdsell 1967: 134).

3.3 CLIMATIC SELECTION: A REVIEW OF THE LITERATURE

3.3.1 Historical Context

Nature or nurture? This has been a recurrent theme in the history human inquiry into the development and growth of living organisms. Only recently have scientists begun to unravel the mysteries of heredity and yet the degree to which morphology and behaviour is determined by the genome or by the conditions under which an organism develops, is still hotly debated. There is no right or wrong in this debate. Both genes and environment affect phenotype - it is the dominance of one factor over another which is the main focus of debate. Yet, the idea that the environment affected the development of animals and humans emerged long before the molecular nature of heredity was

discovered. The concepts of environmental determinism (behaviour or culture determined by the environment) and adaptationism (morphological variation determined by environment) had their origins in the Greco-Roman view that considered both social and natural factors as important developmental effectors (Spencer 1997a). The philosophers and scientists of classical Greece, such as Aristotle (384-322 BC) and Hypocrates (ca. 460-377 BC), argued that many differences between humans could be attributed directly to the environment. Aristotle, for instance, linked the difference between the woolly hair of the Æthiopians (Africans) and the straighter hair of the Scythians to the different climates in which these people lived (*De generatione animalium* cited in (Spencer 1997b: 108). The theories of Hypocrates about the relationship of the environment to variation in morphology and behaviour were to become influential in the Enlightenment period beginning in the 17th century and from there into the emerging field of anthropology in the 18th and 19th centuries (Agelarakis 1997) and can be traced to the works of Carlton Coon in the 20th Century (Harris 1968: 93-94). But the so-called environmental hypothesis or adaptationism was by no means a Euro-specific phenomenon, with references to environmental causes underlying human variation to be found in the early (4th Century BC) literature of India and China (Spencer 1997a). It is simply a direct consequence of a secular and empirical view that places humans within rather than above their environment.

In western science the debate over modern human variation has its roots in Christian theology. The tenets of monogenism: that all people descended from Adam and Eve, only differing because of the different environments they inhabited (see Barton 1797; Buffon 1766; Camper 1772; Stanhope Smith 1788), versus polygenism: the divine creation of separate races, some (those descended from Adam and Eve) more favoured than others (see Caldwell 1830; Homes 1776; Hunt 1864; Morton 1839), have seemingly affected the scientific discourse about human variation to the present day.

3.3.2 Ecogeographic Rules

In 1859 Darwin proposed his theory of evolution in the book entitled *Origin of Species by Means of Natural Selection* (Darwin 1859). The main tenet of this theory is that differences between species (or within widespread species) occur due to the selection for features that better fit an organism to its environment. However, Darwin was to back away from such a strictly adaptationist view of human evolution. In *The Descent of Man and Selection in Relation to Sex* (Darwin 1871), he argued that sexual selection played the major formative role in modern human variation. Indeed, over the past century it has been discovered that natural selection is only one element in the process of evolution. Along with sexual selection, subsequent research has highlighted the importance of stochastic (chance) processes such as mutation, gene flow, genetic drift and founder effect, as well as factors of population structure (Dobzhansky & Pavlosvsky 1957; Fisher 1930, 1937, 1950; Haldane 1948; Mayr 1942, 1963; Wright 1922, 1931, 1939, 1978).

That said, the focus of this thesis concerns adaptation and, in particular, adaptation to climate. As outlined by Mayr:

“it was realized surprisingly early that there is close correlation between the environment and much of geographic variability. In 1833, Gloger devoted an entire book of 159 pages to the subject of *The Variation of Birds under the Influence of Climate*. Bergmann (1847), and J.A. Allen (1877), and others, in notable contributions to the subject, came to similar conclusions long before 1900” (Mayr 1963: 309).

The so-called ecogeographic rules are merely generalisations based on empirical observations of geographic variation in animal species (Mayr 1963). These observations relate to clines in phenotypic traits, such as coat or skin colour, body size and shape, and explain these clines in terms of adaptation to the environment. As Mayr puts it:

“The geographic variation of species is the inevitable consequence of the geographic variation of the environment. ... In the external environment there are principally two groups of factors that may exert a selection pressure on the phenotype: (a) climatic factors and (b) habitat and biotic factors” (Mayr 1963: 311).

He theorised that these two effectors would manifest different patterns of variation. Because climate tends to change slowly over geographic distances, the patterning in variation would tend to be broadly clinal. As biotic and habitat differences tend to be local, and patchy, so would the patterning of the adaptive response to these factors (Mayr 1963: 311). This point will be examined further in Chapter 10.

Although there are several of these "rules" only two are pertinent to this thesis - Bergmann's Rule and Allen's Rule - and these are traditionally linked to climatic, rather than habitat factors. Although they are certainly tendencies, to call them rules tends to imbue them with a greater biological and evolutionary significance than they may truly deserve.

3.3.2.1 Bergmann's and Allen's Rules

In 1847 Bergmann wrote in *Über die verhältniisse der warmeconomie der thiere zu ihrer grosse*, that there appeared to be a general trend for body size in warm-blooded animals to be larger in the colder parts of their range. In other words, an animal's body size was inversely related to the temperature of the habitat in which it lived. Bergmann did not restrict this to a specific level as such, and stated that it occurred among "genera with at least five types." (Bergmann 1847: 686) (author's translation). Most modern writers on the subject, however, limit the effect to geographically widespread species (eg. Mayr 1963: 319).

Thirty years later Allen wrote that as:

“a general rule, certain parts of the organism vary more than does general size, there being a marked tendency to enlargement of peripheral parts under high temperature, or toward the tropics ... This is more readily seen in birds than in mammals ... In mammals it is manifested occasionally in the size of the ears and feet, and in the horns of bovines, but especially and more generally in the pelage” (Allen 1877: 116).

This has become known as Allen's rule and as with Bergmann's rule it is said to operate intra-specifically. It is clear from Allen's article that he felt that the effect was primarily ontogenetic in nature, with hot climates facilitating blood flow to the periphery and cold restricting it, thus accelerating or retarding the growth of the extremities (Allen 1877: 136). Allen also suggested that the effect might apply to humans (Allen 1877: 136-137).

3.3.2.2 How are the rules thought to operate?

In warm-blooded animals (birds and mammals) the changes in body size and shape described by these rules, are traditionally believed to operate to maintain thermal balance within the organism. Thermoregulation is a balance between the heat produced from metabolic processes, and/or heat input from the environment via radiation, and heat lost from the body through radiation, evaporation and conduction/convection (Frisancho 1981: 12-20). In a warm-blooded organism the body mass or volume is responsible for the production of metabolic heat and the skin (body surface) is the major organ of the body responsible for heat dissipation.

The theoretical basis of Bergmann's rule is the simple geometric principle (Fig 3.2), relating surface area to volume (or weight). As the size of a three-dimensional shape increases, the ratio between its surface area and its volume decreases, because surface area rises to the 2nd power, whilst, simultaneously, its volume rises to the 3rd power. Thus a smaller body will have a relatively greater surface area per unit volume than a larger body of the same shape. In terms of thermoregulation, a body with a small volume, or mass, will produce absolutely less metabolic heat and have a higher skin-surface to mass ratio thereby losing heat more rapidly: a situation that would be more advantageous in a hot climate. On the other hand a body with a large mass, and low surface to mass ratio will produce absolutely more metabolic heat and retain it better, thus being of advantage in a cold climate (Frisancho 1981: 21). On the face of it this hypothesis would seem simplistic and has been criticised as such (see section 3.3.5), but Mayr has argued that the close parallelism between body size and measures of temperature in a wide range of species must inevitably lead to the interpretation that "Bergmann's rule is the result of natural selection in favor of an optimal surface to volume ratio..." (Mayr 1956: 106).

But there are other ways of increasing and decreasing body surface area and this is the point of Allen's rule. Animals are not spherical, they have extremities which themselves often have very high surface area to volume ratios and thus may be important to thermoregulation. In a hot climate it would be advantageous to have long, thin extremities and in a cold climate, short stocky extremities. Christopher Ruff has recently studied the relationship of body linearity and temperature, and his research indicates that it may be the diameter of the body (or extremity) rather than its length that is important to changes in surface area to volume ratio, and consequently to thermoregulation (Ruff 1991, 1994) (Fig 3.3). Such changes in shape may well be more important than changes in size and, as Holliday has noted, may obscure evidence of Bergmann-like size clines (Holliday 1997b: 424).

Bergmann-like clines have also been found in some ectothermic animals (reptiles, amphibians, fish and insects), although exactly why such clines are adaptive for ectotherms remains contentious (see the discussions in (Mousseau 1997; Partridge & Coyne 1997; Van Voorhies 1997). The fact that the actual basis of Bergmann's and Allen's rules remains elusive is a major problem. A number of experimental studies have been undertaken to unravel the physiological basis of the ecogeographic rules and these will be discussed in section 3.3.4. Other studies have approached the problem conceptually. Searcy, for instance, has mathematically modelled the body size/temperature relationship and finds that the optimum size of an individual is at:

“that size at which the difference between energy intake and maintenance energy cost per time, scaled to body size is greatest. The model predicts that this optimum size should increase as ambient temperature is lowered and thus provides an explanation for Bergmann's Rule” (Searcy 1980: 590).

3.3.3 Empirical and Experimental Studies on Non-Human animals

3.3.3.1 Introduction

As ecogeographic studies were first examined in the field of zoology and are still being assiduously researched, it is pertinent to review the evidence for climatic selection in the non-human, animal kingdom, before moving on to studies focusing on humans. If ecogeographic rules are found to apply to other animals then any evidence for these rules in humans is strengthened. However, the rules have been challenged and these criticisms will be discussed in Section 3.3.5.

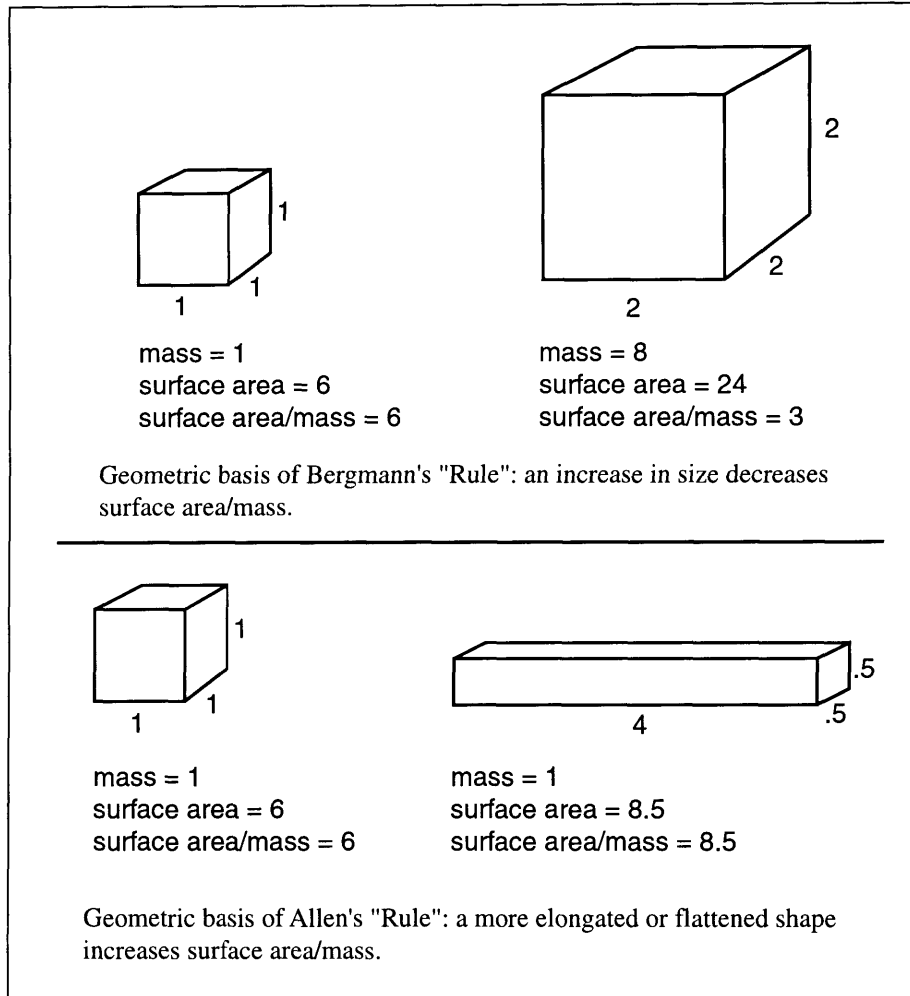


Figure 3.2: The geometric basis of Bergmann's and Allen's rules, after Ruff 1994.

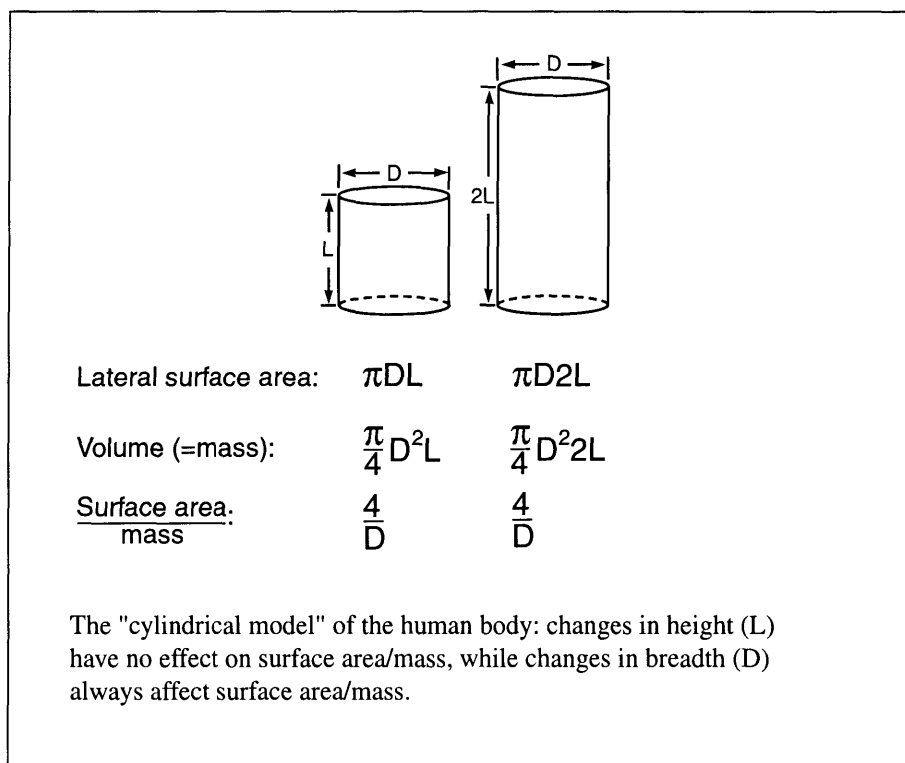


Figure 3.3: The cylindrical model of the human body, after Ruff 1991.

Table 3.3: Empirical studies finding evidence for ecogeographic rules in non-human animals.

Reference	Taxon	Comments
Bergmann 1847	Endotherms (various)	Established that body size is inversely related to environmental temperature.
Allen 1877	Endotherms (various)	Established that the relative length of peripheral structures is positively related to environmental temperature.
Rensch 1936	Birds and Mammals	Found that Bergmann's and Allen's rules were widely applicable in birds and mammals, but it depended on "other things being equal".
Hamilton 1961	Birds	Examined how various factors including temperature and humidity, length of foraging day and vegetation density were related to body size and wing length in birds. Confirms the existence of ecogeographic clines, however finds that "ecogeographic variation at the inter-specific level is generally achieved by the operation of more than one selection force" (188).
Lindsey 1966	Ectotherms (various)	The author finds that "among fish and amphibian faunas the proportion of species with large adult body size tends to increase from the equator towards the poles" (460). The effect was weak or absent among reptiles. He argues that as experimental evidence suggests cold-blooded animals reared at lowered temperatures tend to grow larger and live longer, that selective pressure need not be involved ie. the effect is ontogenetic (461).
Brown & Lee 1968	Woodrats	Finds evidence for the operation of Bergmann's rule in Woodrats.
James 1970	Birds	Finds that both temperature and moisture were important determinants of body size in birds, with smaller body sizes found in hot, moist regions and larger body size in cooler or drier areas
Barnett 1977	Grey Squirrel	Body size in <i>S. carolinensis</i> conforms to Bergmann's rule, but other factors such as feeding adaptations affect head size (often used in other studies as a de facto measure of body size).
Burnett 1983	Bats	Finds that in the bat species, <i>Eptesicus fuscus</i> , wing and skull length correlated more closely with moisture than temperature. He argued this was due for the need to conserve moisture in arid regions.
Ralls & Harvey 1985	Voles; Weasels	Finds that the size of vole and weasel species increases with latitude.
Yom-Tov, Green, & Coleman 1986	Brushtail Possum	Body size clines in the Brushtail Possum introduced into New Zealand conform to Bergmann's rule and these clines were reached within 50 years of introduction.
Yom-Tov & Nix 1986	Marsupials	Authors find that size variation in the body and skull of five Australian mammals (echidna, brush-tail possum, eastern grey kangaroo, western grey kangaroo and red kangaroo) conforms with Bergmann's rule. The kangaroos also conform to Allen's rule, with relatively longer extremities in warmer areas.
Baumgardner & Kennedy 1993	Kangaroo Rats	Some evidence for Bergmann's rule in various species of kangaroo rat, but authors conclude that factors other than temperature may be more important in determining body size.
Ellison <i>et al.</i> 1993	Pouched Mice	Geographic variation in body size was found to correlate with latitude, temperature and seasonality, supporting Bergmann's rule, however, these correlations also co-varied with rainfall. Allen's rule was not confirmed.
Fooden & Albrecht 1993	Macaques	Evidence for Bergmann's rule in skull size of crab-eating Macaques in some areas, however, exceptions to the rule where populations subject to long term isolation.
Kratter 1993	Yellow-billed cacique	Bergmann's rule confirmed.
Stone 1993	Bees	In studying thermoregulation in four tropical species of solitary Bee, Stone finds that in <i>Amegilla sapiens</i> body mass increases with altitude, which he takes to support Bergmann's rule.

Table 3.3: Empirical studies finding evidence for ecogeographic rules in non-human animals.

Reference	Taxon	Comments
Yom-tov 1993a	Rock hyrax	Rock Hyrax showed morphological adaptation to heat but not to cold.
Holcik & Jedlicka 1994	Bitterling (fish)	Bergmann's rule demonstrated for fishes and at the species level in the cyprinid fish <i>Rhodeus sericeus</i> .
Rasmussen 1994	Imperial Shag	Finds some evidence for Bergmann's rule in South American Imperial Shag with some exceptions due to possible isolation. Allen's rule also supported.
Taylor & Gotelli 1994	Minnow	Find evidence for Bergmann's rule in Minnows in a western clade but not in an eastern clade.
Wyllie & Newton 1994	Sparrowhawk	Body size increases from south to north in British Sparrowhawks as predicted by Bergmann's rule.
Kaspari & Vargo 1995	Social Insects	Colony size rather than individual size is an adaptation to temperature, however, colony size is related to resistance to over-wintering starvation rather than thermoregulation.
Sand <i>et al.</i> 1995	Moose	Bergmann's rule is confirmed for body weight (mass), but not body size (skeletal size). This is attributed to differential fatness as an adaptation to colder climates.
Smith <i>et al.</i> 1995; Smith & Betancourt 1998	Wood-rats	Body size in fossil Wood-rats, estimated from coprolite size, correlates with changes to climate over the last 25000 years in accordance with predictions based on Bergmann's rule.
Blackburn & Gaston 1996	Birds	Body size in bird species in north and south America show clinal variation in accordance with Bergmann's rule, however other ecological factors apart from temperature may be involved - eg. energy availability and species richness (diversity).
Gay & Best 1996	Puma	Geographic variation in size in pumas from north and south America is in accordance with Bergmann's rule.
Paterson 1996	Macaques	Body size and body shape in captive Japanese macaques in colonies in Oregon and Texas varied in accordance with both Bergmann's and Allen's rules with the northern troop being larger with relatively shorter limbs than the southern troop. Differences in morphology and growth rates were attributed to the different climatic conditions under which the troops lived.
Quin <i>et al.</i> 1996	Marsupials	Body size in the Sugar Glider and Squirrel Glider was found to vary inversely with climate as might be predicted by Bergmann's rule, but other factors such as isolation-by-distance and seasonality were also found to be significant factors in geographic variation in body size. Body size was found to be larger in seasonal environments where food resources are less predictable.
Sharples <i>et al.</i> 1996	Rabbit	Body size in the European rabbit in western Europe and north Africa varies with temperature in accordance with Bergmann's rule. This would argue against the common practice of conferring sub-specific rank to geographic variants in this species.
Slotow & Goodfriend 1996	Cape Sparrow	Cape sparrows in the Namib were smaller than those found in the cooler Transvaal as predicted by Bergmann's rule. Allen's rule was not confirmed.
Bried & Jouventin 1997	Sheathbill	Both Bergmann's and Allen's rules are substantiated in Black faced Sheathbill populations.
Merila 1997	Greenfinch	Most skeletal measurements in the Greenfinch were in accordance with Bergmann's rule being positively and significantly correlated with latitude.
Heinze <i>et al.</i> 1998	<i>Leptothorax acervorum</i> (Ant)	Body size in <i>Leptothorax acervorum</i> was found to be larger in colder regions of their range confirming Bergmann's rule in an ectotherm.
Ravosa 1998	Slow Loris	Evidence is found for Bergmann's rule in slow lorises.

3.3.3.2 Empirical studies

There is a large body of work on Bergmann's and Allen's rules in the zoological literature, and it has been found to apply to both endotherms and ectotherms. Table 3.3 presents a summary of the results from a selection of studies where the rules have been confirmed. This is a far from comprehensive list, but a more detailed review is unnecessary in the present context. In general, whilst there is an extensive literature of an empirical nature to confirm the existence of Bergmann's rule, the exact nature of the phenomenon is still debatable. In many cases researchers make the thermoregulatory hypothesis implicit, whereas others question this, and specifically test other possible models such as species diversity (richness), range size and annual resource variation to account for the observable geographic variation in body size (see Table 3.3 for references).

For Allen's rule, however, far fewer empirical studies have been published, probably because it is easier and faster to measure for size - be it body weight, body length, skull length, or whatever is deemed the most useful measure for a particular species - than it is to measure the length of various extremities. There has also been far less discussion about the underlying adaptive significance of clines in extremity length as they are generally seen as an extension of Bergmann's rule (see Mayr 1963): 323).

3.3.3.3 Experimental studies in non-human animals

Studies that compile empirical evidence for the operation of ecogeographic rules in nature can only demonstrate that geographic clines and correlations between climate and morphology exist, but cannot elucidate the underlying causes - be they thermoregulatory or otherwise. The search for causes has been undertaken using experimentation. These studies have tested specific hypotheses regarding the effects of environmental factors such as temperature on growth, or on the adaptive advantage of different body morphologies. These studies tend to fall into two broad categories. 1) Raising one or more generations of animals under different temperature regimes and 2) keeping "races" (usually artificially selected breeds) of a species with different body shapes at high and/or low temperatures to observe differential survival rates. The first method tends to highlight the plastic, ontogenetic effects of temperature on the growth and development of the experimental subject, although selection effects can also be observed in generational studies. The second method highlights the adaptive and selective value of particular body morphologies to contrasting temperature regimes.

There is a century long history of experimentation into ecogeographic rules (eg. Allee & Lutherman 1940; Allee & Schmidt 1951; Emery *et al.* 1940; Furuyama & Ohara 1993; Harrison 1958; Harrison *et al.* 1959; Ogle 1934; Ray 1960; Riesenfeld 1973, 1976, 1980, 1981; Siegel *et al.* 1977; Sumner 1909, 1915; Sundstroem 1922, 1927; Weaver & Ingram 1969).

Although most of these experiments were testing solely for ontogenetic effects in one generation, the results of their studies are instructive in laying the probable foundation for genetically based size clines found in nature. Of course such strictly controlled growth experiments have been restricted to non-human animals, and usually those that either reproduce and/or mature at a rapid rate, however, studies examining the adaptive advantages of body shapes have been conducted on humans and these will be reviewed in Section 3.3.4.5.2.

3.3.3.3.1 Testing for Bergmann's Rule

There are major difficulties in comparing the published studies because of a lack of consistency in methodology and reporting of results. There are marked differences in what animals were studied and how the animals were raised: the age at which they were entered into the experiment, the temperatures under which they were raised and the nutrition they were given. In studies on rats and mice (the most common test subjects) it has generally been found that subjects raised at higher temperatures attain lighter body weights than those raised at lower temperatures (Sumner 1909, 1922, Ogle 1934). In Ogle's study her cold-room mice grew at about the same rate as her controls and achieved the same end weight, but her hot-room mice had a lower growth curve and attained a lower end weight than either the controls or the cold-room mice (Ogle 1934: 637). She also found differences in body length to weight ratio between the cold and hot groups - the cold group being heavier for their length than the hot group (Ogle 1934: 638), a result also reported by Sundstroem (1927: 332). Emery *et al.* (1940), however, conducting experiments with rats, found that the body size of the cold reared group was smaller (in length and mass) than in the controls. This result would appear to contradict Bergmann's rule, however the researchers discovered that there was a suite of differential effects particularly on the size of the organs, with enlargement in some and reduction in others (Emery *et al.* 1940). The negative effect of cold on body size was also reported by Sumner (1909) and later by Riesenfeld (see below) and is apparently due to the test subjects being exposed to temperatures well below optimal causing severe stress to the animals.

Beginning in the 1970s Riesenfeld conducted a series of experiments on rats. His interest was specifically to link this work to aspects of human evolution (Riesenfeld 1973, 1976, 1980, 1981). In his 1973 study he found that body weight decreased in rats raised under both the extremes of cold and heat. Because of this, his study emphasised changes to body shape rather than changes in absolute weight and size. In his later papers (Riesenfeld 1980, 1981), however, he was more interested in whether differences in body size and shape conferred selective advantage in hot and cold environments. He raised groups of large and stocky Buffalo strain rats, and smaller more linear Fisher strain rats under hot and cold conditions. He found that on average the larger Buffalo rats survived longer in extreme cold than Fisher rats, with converse results in extreme heat. This he attributed mainly to differences in body mass and size, confirming Bergmann's rule

(Riesenfeld 1980). He went on further to prove that this effect was not due to some genetic factor unique to the particular strains of rat by raising groups containing both large and small bodied Buffalo and Fisher rats (Riesenfeld 1981). In both strains the larger bodied groups survived longest in cold and the smaller bodied groups longest in heat.

In a more recent experiment Furuyama and Ohara selectively bred a strain of rats to resist high temperatures (Furuyama & Ohara 1993). One of the notable effects was a progressive decrease in body size in the early generations. The authors, however, argue that the more efficient heat dissipation in their rats may have been due to the ability to "mobilize and evaporate body fluids" (Furuyama & Ohara 1993: 957) rather than having an increased surface area to volume ratio.

Growth experiments have also been undertaken on other animals, for instance Allee and Lutherman (1940) and Allee and Schmidt (1951) found that the body weight of chickens grown at high temperatures was less than those raised at lower temperatures and Weaver *et al.* (1969) found a similar effect in swine.

The basis for the rules has also been tested for ectotherms. Ray (1960) conducted his own experiments as well as summarising the work of other researchers. He found that over a wide range of ectothermic (or poikilothermic) animals, Bergmann's rule was found to apply to 75% of species (Ray 1960: 101). He was, however, cautious about the significance of the effect, as the arguments for the physiological basis for Bergmann's rule were formulated in terms of endothermic energetics which, of course, do not apply to ectotherms.

3.3.3.3.2 Testing for Allen's rule

Many of the studies mentioned above also examined the effect of temperature on the relative length of appendages (Allen's rule). It has been found that in rats and mice tails grew longer and feet larger when the animals were raised at higher temperatures (Harrison *et al.* 1959; Ogle 1934; Sumner 1909, 1915; Sundstroem 1922, 1927). Harrison *et al.* (1959), for instance, reported a two-centimetre difference in tail length in mice reared at 90°F over those raised at 70°F. This effect on appendage growth has also been observed in studies on chickens (Allee & Lutherman 1940), swine (Weaver *et al.* 1969), rabbits (Mills 1945: 98) and a range of ectotherms (Ray 1960). Harrison also studied the importance of the rodent's tail to its thermal balance. He exposed a group of mice whose tails had been amputated and a control group (non-amputee) to heat stress. The amputee group had a significantly shorter survival time (Harrison 1958). The experiment, this time using rats, was repeated by Riesenfeld, who found that the tail was only effective in heat dissipation when ambient temperature was below that of the rats' body temperature (Riesenfeld 1980: 38-39). But Riesenfeld was to contradict the earlier studies that claimed that animals grown at high temperatures had longer tails. He found instead that the method of measuring the tail (anus to tip) was faulty, as anus position depended on the size of the

internal organs and was not a fixed point. In his study groups he found that tail length in his hot group did not increase, however, he did find a real and significant shortening of the tail in the cold group (Riesenfeld 1973: 452). He also found a real and significant shortening in the long bones and an increase in bone robusticity in his cold reared group, repeating a finding by Steegmann and Planter (1968: 28). Overall Riesenfeld concluded that:

“A considerable number of cold-specific changes in experimental cold exposure of rats resembles conditions which in human populations are generally considered as cold adaptive. Even if one fully recognizes the complexity of the problem shared by all biomedical experimentation, it would be impossible to consider all resemblances as mere accidents or superficial mimicry. More likely the identical reactions represent physiological and morphological responses to cold stress producing phenotypic changes in the experiment and responding to selective pressures in the phylogeny” (Riesenfeld 1973: 453).

In later papers, however, Riesenfeld stepped back from this emphasis of Allen's rule arguing that it is body size and weight rather than changes in appendage length that are the critical adaptations for thermoregulation (Riesenfeld 1980, 1981).

3.3.3.3 Testing for the cold-engineered face

In 1950 Coon, Garn and Birdsell argued that the typical features of the Mongoloid face were the result of long-term selection against frostbite injury. Steegmann and Platner's (1968) paper mentioned above was aimed specifically at examining this theory through experimentation in rats (see section 2.5.4.5.3). A sample of 24 male Sprague-Dawley rats were exposed to cold (starting at 13°C, dropping to 5°C) for 90 days and these were compared with a control sample of 20 rats. Three control rats and 13 cold-room rats died during the experiment (Steegmann & Platner 1968: 18). Measurements of both groups found that the cold room rats exhibited narrower noses, shorter crania and shorter-broader malars than the controls (Steegmann and Platner 1968: 28). These changes parallel the facial form of some Arctic populations, however the authors necessarily distance themselves from any contention the Mongoloid facial form is merely an ontogenetic response to cold (Steegmann & Platner 1968: 38-39) and, indeed, further study by Steegmann on human subjects, found that this facial morphology conferred no apparent thermoregulatory advantage.

3.3.4 Empirical and Experimental Studies on Humans

3.3.4.1 Introduction

Historically, climate was viewed as one of the primary causes of variation between human "races" (see section 2.5.1), but it was not until the 1940s and particularly the 1950s that scientists began to systematically explore environmental factors such as temperature and humidity as causative agents in human variation. The variation examined in these studies was both anatomical and physiological.

The studies reviewed here fall into four broad categories. The first are conceptual studies that review evidence from observational or experimental studies and fit this evidence into a model for human evolution. The second type of study is of an empirical nature relating geographic variation in body morphology with geographic variation in climate (although latitude is sometimes used as a proxy). These studies have used either qualitative methods (pictorial or clinal) and/or quantitative methods (statistical theory - in particular correlation), to ascertain the degree of coincidence between morphology and climate (see Chapter 5). Some of these studies link these correlations to long-term evolutionary processes, whilst others explain their operation as reflecting developmental plasticity.

The third category examines the problem in a different way. These studies have focused on short term secular changes in body morphology using migrant populations. Whilst these studies tended to emphasise ontological causes for morphological change between generations, rather than long term evolutionary change, they have also identified certain aspects of body morphology that are less developmentally plastic, such as relative body proportions.

The final category contains experimental studies. Of course the type of experiments conducted on animals are ethically and morally impossible on humans, but studies linking body morphology and temperature tolerance have been conducted.

3.3.4.2 Conceptual studies

Following on from the early research into animal populations, physical anthropologists examined human populations for evidence of climatic selection. Although there were early suggestions by Allen (1877), Ridgeway (1908) and Buxton (1923) linking morphological differences between human groups with climate, it was Carlton Coon and his collaborators who fully articulated the theory that some of the variation between "racial" groups was due to adaptation to factors of their habitual environments. These factors included climate, altitude, diet and disease. Their claims about the first of these

will be summarised here.

Coon, along with Joseph Birdsell and Stanley Garn, (Coon 1955, 1962; Coon, Garn, and Birdsell 1950) argued that variation in many human traits was due to climatic selection. Differences in body proportions, for instance, were linked to thermoregulation. Adaptations to a hot, dry climate included a linear build (although not necessarily tall stature) with relatively long and thin arms and legs, and a short trunk. The critical factor being:

“for the organism to present the maximum skin surface area in proportion to mass and weight to the external environment, thus permitting a maximum cooling surface for evaporation” (Coon, Garn, and Birdsell 1950): 37).

At the other extreme, adaptation to cold, it was argued, produced moderate stature, thickset bodies with broad, deep chests and short, thick limbs and digits. This body shape reduced surface area to weight ratio thereby decreasing heat loss (Coon, Garn, and Birdsell 1950: 43).

Testing the hypotheses put forward by Coon, Garn and Birdsell has always been conceptually limited by anthropometric methodology. There has been a lack of standardisation in sampling procedures, in the type of measurements taken and methods used to take them, and in subsequent analytical methodologies. Moreover, many studies have used data recorded by more than one observer, as well as data that were originally gathered with other research objectives in mind. The measurements taken may therefore not be the most appropriate ones to study ecogeographic correlations. Even in studies that are purposely carried out to explore ecogeographic adaptations, the need to maximise sample size through the utilisation of historical data has necessitated the use of the standard range of anthropometric measurements. Other major problems include the issue of whether the groups sampled were breeding populations, were randomly sampled, contained few individuals that were closely related, were of comparable ages and had equal access to nutrition. Such considerations are sometimes addressed, but the ideal of gathering enough quality data for statistical purposes is often unattainable in the real world. It should be noted that many of these considerations apply to this present study as well.

Coon's theories attracted critics from various quarters, the most vocal being Scholander, Irving and Wilber. Their main criticism was that humans, having the ability to adapt to changes in climate through culture, are buffered from climatic selection (Irving 1957; Scholander 1955; Wilber 1957) (see section 3.3.5 for a more detailed review of their critiques).

In 1960 Baker published an influential paper entitled "Climate, Culture and Evolution" that aimed for a synthesis between these competing forces in human evolution. Combining the observational and experimental data collected by himself and others,

Baker argued that any adaptation to climate during human evolution must have necessarily occurred within a cultural context and that climate and culture interacted to affect selection (Baker 1960: 5-6). He examined a range of theoretical selective conditions through an investigation of the geographic distribution of surface area to weight ratios in human populations. He found that there was clear evidence for climatic selection operating in the variation in this trait but that culture-interactions and the physiology of thermoregulation explained why there was not a perfect fit between climate and surface to weight ratios in humans (Baker 1960). This multifactorial theme was also pursued by Hulse (1960), in a paper published in the same year.

In a later article, Baker went on to challenge the anthropological community to test three possible hypotheses regarding human adaptation to the environment (Baker 1966a). These included:

“1. Population differences in genotype including gene frequency differences are the product of environmental adaptation (including culture as part of the environment).

2. The longer a population has lived in a set environment, the greater the probability that their genotypic eccentricities are a product of adaptation to the environment.

Subhypothesis

A. Ecologically stable populations will be more likely to show genetic adaptation than ecologically unstable units.

B. Genetic differences are more likely to be related to the stable stresses of the environment such as climate and disease than to the more changeable stresses such as produced by culture.

3. Many phenotypic variations in man are not the product of genetic adaptation” (Baker 1966a): 86).

Little and Hochner (1973) were to argue, however, that the effects of cultural buffering might not be as important as Baker has suggested. As they note, even with our modern technology it is impossible to fully protect against the influence of climate and for most of our evolutionary history we have had even less cultural protection (or buffering) than we do now. This suggested to the authors that some of the patterning in body size and shape variation that we see in modern groups, was due to the selective pressures of climate on our hominid ancestors (Little and Hochner 1973: 1).

Perhaps the seminal work in the application of ecogeographic rules to humans was that of D.F. Roberts (Roberts 1952, 1953, 1973). Like Baker he constructed a theoretical framework to explain the geographic patterns in human physiology and anatomy that his

research had revealed. In evolutionary terms he postulated that climate might have affected body morphology by influencing "the genetic potential (the genotype) of the organism" (Roberts 1973: 3). This could be the direct consequence of "the selection of those morphological, physiological, mechanical, and other features which make for greater organic efficiency in a given environment" or through an influence on cell development and function (Roberts 1973: 3). It may also work indirectly, either "by influencing the size of population a given region will support, the effectiveness of mutation and selection being dependant on the size and breeding structure of the population" or "by influencing the degree of accessibility of a population, and hence the degree of isolation in which it develops" (Roberts 1973: 3). Further, he argued that climate may cause ontogenetic modifications to phenotype either by the "direct modification of gene manifestation, induced by such factors as temperature or humidity" or indirectly by determining the distribution factors that can alter development, such as nutrition and disease (Roberts 1973: 3).

Such conceptual studies laid the foundations for further research into ecologically based studies of human evolution.

3.3.4.3 Ecogeographic Studies: Whole Body

3.3.4.3.1 Clinal and Statistical Studies on Worldwide Population Samples

Over the same period as conceptual studies were being published, other researchers were gathering data and examining the applicability of ecogeographic rules to various modern human populations. Published in the same year as Coon, Garn and Birdsell's work, were two papers by Eugène Schreider in *Nature* and *l'Anthropologie* (Schreider 1950a, 1950b). Schreider examined the weight to surface area (W/SA) ratio (kg/m^2) for 16 male and 4 female groups, spanning temperate to tropical areas from Western Europe to Southeast Asia and Central America. Without resorting to statistical methods, he noted that there was "obviously a decline of the value of the ratio as we proceed from temperate to tropical regions" (Schreider 1950a: 286). The same trend was not found in his female sample, although it was too small to draw any firm conclusions. He argued that W/SA ratio was linked with body heat regulation, and that an excess of body-surface to weight (or deficiency of mass to surface area) was advantageous in a hot climate (Schreider 1950a: 286). He also noted that similar ratios were attained by the tall and extremely linear Somalis of Northeast Africa, and the small-statured and relatively stocky Otomies of Mexico. Both have low weight to surface area ratios but one group has achieved this through an increase in surface area relative to weight the other by a decrease in overall weight relative to surface area. In following papers (eg. Schreider 1964, 1975) Schreider expanded his sample size and continued to argue the case for W/SA being the most important factor in climatic selection of body shape, although he could not explain why the relationship was not repeated in the female sample.

As mentioned in the previous section the most influential (certainly the most cited) contributor to this field of study is D.F. Roberts (Roberts 1952, 1953, 1973). His 1952 paper examined ecogeographic variation in body size (weight and stature) and basal metabolism in modern human populations. Roberts' results demonstrated that basal metabolism is inversely related to ambient temperature, but it also directly related to weight. Further, he found that there were "intrinsic" differences in basal metabolic rate between human groups that could not be explained through a relationship with weight or temperature (Roberts 1952: 170). But despite such differences between groups, Roberts concluded that taken overall:

“in order to facilitate the balance of human body-heat exchange, under those conditions in which heat-loss is more difficult, less heat is produced (on account of reduction in the amount of body tissue) and the ratio of surface area to weight (ie the ratio of potential heat-loss to potential heat-production) is increased. Thus the functional mechanism underlying Bergmann's and Allen's rules, postulated for the relationship of body size and proportions with environment in warm-blooded species, would appear to be confirmed when applied to man” (Roberts 1952: 170).

In two further papers Roberts expanded on his hypothesis (Roberts 1953, 1973). The earlier paper focussed on body size, temperature relationships among and between continental populations. He examined data from 116 male and 33 females groups. The minimum sample size was 20 individuals and age range was limited to between 20 and 40 years. In an examination of the geographical distribution of weight he found that there was a tendency for "very high" weights to occur in cold areas and "very low" weights being more prevalent in hotter areas (Roberts 1953: 536). "Medium" weights, in contrast, were found not to be as confined in their distribution. Within continental areas, for instance Europe and eastern Asia, weights tended to increase from south to north (Roberts 1953: 537). Although the pattern was not so clear-cut in the Americas and Africa, Roberts argued strongly that there was:

“an underlying inverse relationship between weight and mean environmental temperature discernible not only when all mankind is considered but also within continental groups of man, and that differences in level occur among continental groups” (Roberts 1953: 539).

The results of his statistical analysis were repeated in his 1973 paper and will be reviewed below (see Table 3.4). As with his other studies he found a significant relationship between weight and temperature in both his male and female samples, and only a weak relationship between stature and temperature which disappeared when weight was held constant (Roberts 1953: 543). He also calculated the correlation coefficients for his African, American, Eastern Mongoloid and European sample groups and also found significant negative correlations between weight and temperature, but no

significant correlations between temperature and stature (Roberts 1953: 547).

He suggested three testable reasons for the correlation between weight and temperature: 1) differences in body shape or distribution of mass to stature; 2) the need to vary body heat production in different temperature regimes and 3) the need for increased insulation in cold climates to reduce heat loss (Roberts 1953: 550).

Table 3.4: Summary of correlations between average annual temperature and basal metabolism and metrical variables of body size and shape in a worldwide population sample of males and females, adapted from Roberts, 1973.

Variables	Male		Female	
	n	r	n	r
Basal metabolism (cal/24hr)	160	0.736***	?	0.845***
Weight	116	-0.600***	33?	-0.809***
Weight (stature held constant)	116	-0.538***	33?	-0.704***
Stature	116	-0.351***	33?	-0.587***
Stature (weight held constant)	116	0.164	33?	0.208
Sitting Hgt	285	-0.428***		
Rel Sitting Hgt	285	-0.619***	?	-0.654***
Rel Calf Circ (calf/tib)	?	-0.558*		
Calf/thigh (tib/fem)	?	0.479*		
(Anti)brachial Index (rad/hum)	?	0.586***		
Rel Biacromial	?	-0.557***		
Rel Bicristal (bi-iliac)	?	-0.823***		

(* p significant at 5%; ** p significant at 1%; *** p significant at 0.1%; ? sample size uncertain.)

In his 1973 paper "Climate and Human Variability", Roberts extended his analysis beyond body size to body proportions. His results are summarised in Table 3.4. For his worldwide sample Roberts stated that only indigenous groups were included (ie. no recent migrants), however no indication of the time depth of the occupation of these indigenes was included. Whilst the overall sampling methodology followed that of his previous studies the actual sample sizes for some of his variables were not stated (Roberts 1973).

His conclusions regarding basal metabolism, weight, stature and temperature were repeated from his earlier study. Whilst he noted that despite the significant correlation between temperature and weight a direct relationship cannot be assumed, he went on to argue that if:

“indeed lower weights are advantageous in warmer areas, then so long as that condition is attained, it appears immaterial whether it is attained directly or indirectly ... Further, if nutrition were the cause, one might expect a certain nutritional influence during the growing period, affecting stature, for example, so that elimination of the stature factor should markedly reduce the correlation between weight and temperature; this clearly does not occur” (Roberts 1973: 7).

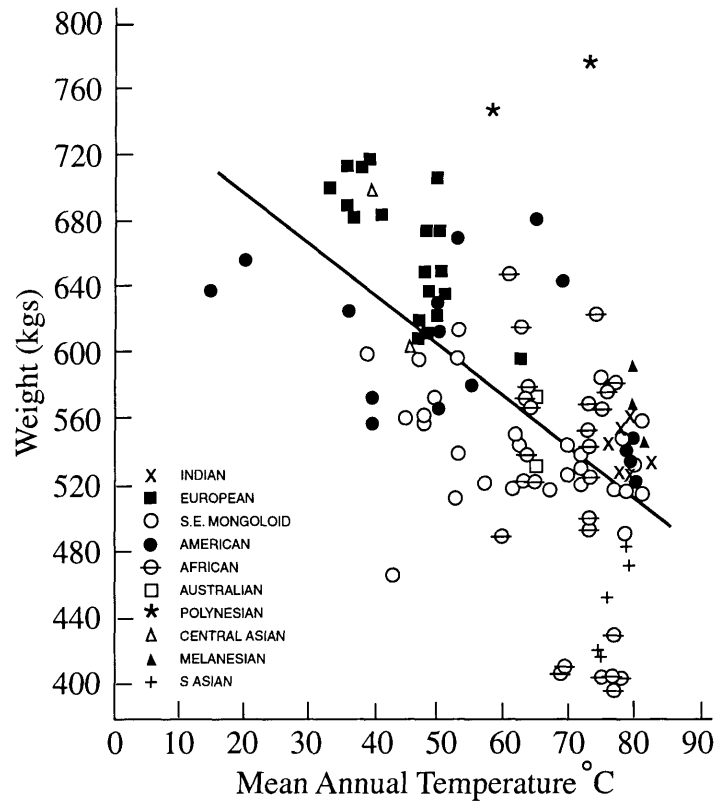


Figure 3.4: Relationship of weight and mean annual temperature in male indigenous groups, after Roberts, 1953: 543.

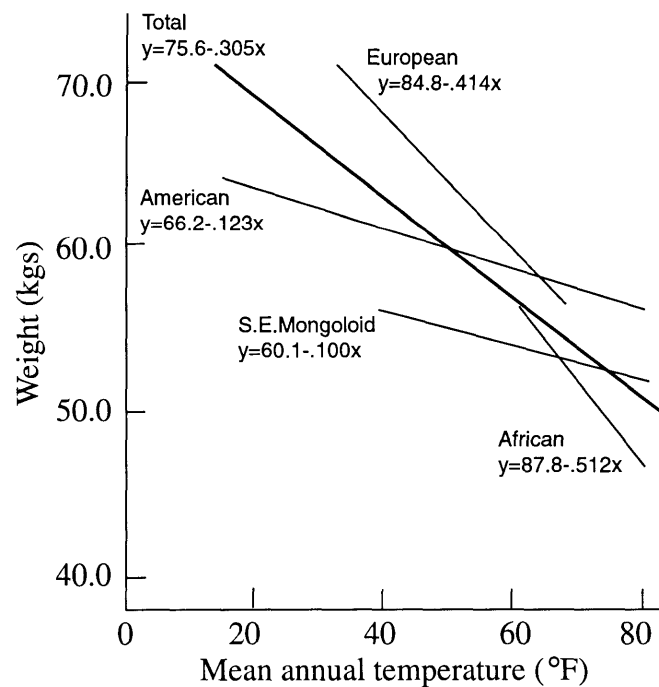


Figure 3.5: Total regression of weight upon mean temperature, and some of its component intravarietal regressions, after Roberts, 1953: 548.

Interpreting his results relating body proportions to temperature, Roberts argued (following Allen's rule) that a low value for relative sitting height represented an adaptation to a tropical climate. Supporting his contention, his results reveal that the population groups with the longest period of residence in the tropics (eg. Africans), had the lowest values for this ratio. High values, meanwhile, were typical of temperate or Arctic groups, or groups that had recently migrated from such regions (Roberts 1973: 8-9). He also found evidence for Allen's rule in the relative limb lengths of his sample groups. Legs became longer relative to stature, and the distal limb segments became longer and narrower with increasing temperature (Roberts 1973: 10). A similar effect is seen in the entire upper limb, however it was clear that the distal limb segment increased in length with increasing temperature to a greater degree than the proximal segment. Roberts also reported that relative arm length (as measured by relative span) and the antibrachial index (radio/humeral index) increased with increasing temperature (Roberts 1973: 10). All these variations in limb length, he argued, increased the skin surface area relative to body volume (as measured by weight), and were thermoregulatory adaptations.

However as a caveat, Roberts warned against a too specific interpretation of the correlation coefficients, saying instead that their:

“interpretation ... should be guided rather by the direction in which they point than by their actual numerical values. The various body characters considered are by no means independent and represent the outward and visible signs of underlying biological factors which, were they extracted, might show closer correlation with climate” (Roberts 1973: 13).

Another study to use a worldwide population sample was that of Walter (1976). His sample included 3,375 groups for stature, and 431 groups for weight. His body shape ratios included Rörher's Index (kg/cm^3) and surface area to weight ratio. He calculated coefficients of correlation between his anthropometric variables and annual average temperature and altitude. His results for the temperature variable are summarised in Table 3.5.

Although the correlations revealed Bergmann-like size clines, particularly for weight, he found there was little evidence to suggest thermoregulatory adaptations were involved. Instead, he argued that it was more likely to be linked to the geographical distribution of nutritional factors, especially protein and calorie supply during childhood (Walter 1976: 252-261).

Table 3.5: Summary of correlations between body size and shape variables and temperature and altitude in a worldwide sample of males, adapted from Walter, 1976: 244-245.

Variables	n	Stature	n#	Weight	Rörher's Index	SA/W
World	3,375	-0.19***	431	-0.50***	-0.21***	0.43***
European	1,260	-0.37***	105	-0.71***	-0.43***	0.68***
African	979	0.21***	141	0.13	-0.03	-0.04
Asian	648	-0.29***	97	-0.41***	-0.11	0.30***
Indian##	355	-0.31***	51	-0.35*	-0.20	0.32*
Aust-Mel	91	-0.27**	28	-0.44*	-0.18	0.37
Pygmy	42	0.16	9	0.40	0.39	-0.44

(* $p \leq 0.05$ ** $p \leq 0.01$ *** $p \leq 0.001$; # numbers in parentheses refer to sample size. The first "n" refers to the sample size for stature, the column for "n" refers to all other variables. ## Unsure whether "Indianide" refers to Southern Indians or Native Americans, although given the range of temperatures used to calculate the sample's regression, it is likely to be the latter. See Figures 1-5 in Walter, 1976: 246-248.)

In his study on the influence of climate on cranial capacity and cranial shape, Beals and his co-workers gathered data on a range of anthropometric measurements and indices from 82 population groups. These were correlated against a variable designated "climate zone", which numbered from dry heat (1) to dry cold (5) (Beals *et al.* 1984: 308, Table 6). Not all measurements were available for all groups and the results of the correlations for the body measurements are reproduced in Table 3.6.

Table 3.6: Summary of correlations between body size and shape variables and climate zone in a worldwide sample of males, adapted from Beals, 1984: 308, Table 6.

Variable	n	r, p
Weight	52	0.38**
Stature	82	-0.05
Surface Area#	52	0.27*
Surface Area/Weight	52	-0.47***
Ponderal Index	52	-0.46***

(* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; # surface area calculated using the formula of Brown and Bregelmann, 1965, see Beals *et al.*, 1984 for full reference.)

The authors reported modest correlations between their body variables and climate zone, the highest being for Ponderal Index. Their correlations for cranial variables were stronger leading the authors to conclude that human head size and shape was under greater climatic control than the body as a whole (Beals *et al.* 1984: 312). Their results for cranio-facial variables will be discussed in later sections.

In 1991 Ruff examined the ecogeographic correlations of bi-iliac breadth and relative bi-iliac breadth. He reported correlations of $r = 0.907^{***}$ between bi-iliac and latitude on a pooled male and female sample, with males alone producing a correlation of $r = 0.895^{***}$ and $r = 0.919^{***}$ in females (Ruff 1991: 86). The correlations for relative bi-iliac breadth

were somewhat weaker than this being $r = 0.643$ on the pooled sample, and $r = 0.680$ and $r = 0.782$ (significance level not reported) on males and females respectively (Ruff 1991: 87).

The most recent study of ecogeographic correlations in a worldwide sample is that of Katzmarzyk and Leonard (1998). Building upon Roberts' database, Katzmarzyk and Leonard's analysis included 223 male and 195 female samples (1998: 485). The anthropometric variables used were weight, body mass index (BMI), surface area to mass ratio (SA/Mass) and relative sitting height (Katzmarzyk & Leonard 1998: 486). Using bivariate regression and correlation they examined the covariance between these variables and mean annual temperature. They found that weight, BMI and relative sitting height varied inversely with temperature, and SA/Mass varied directly with annual temperature (Katzmarzyk & Leonard 1998: 487 - 488). The results of their study are reproduced in Table 3.7. Although all their correlations are very highly significant none is as strong (ie. explain as much covariance) as those produced in Roberts' study. This discrepancy, the authors postulated, was due to a secular increase in weight in some of the more recently collected samples included in their study. They find that this weight gain was likely due to the adoption of a highly refined, western diet by populations used to a much lower calorie intake (Katzmarzyk & Leonard 1998: 493).

Table 3.7: Summary of correlations between body size and shape variables and mean annual temperature in a worldwide sample of males and females, adapted from Katzmarzyk and Leonard, 1998: 485, Table 3.

Variables	n	Male		Female	
		n	r^*	n	r^*
Weight	223		-0.27	154	-0.28
BMI	222		-0.22	153	-0.30
SA/Mass	222		0.29	153	0.30
Rel Sit Height	94		-0.37	71	-0.46

(* $p \leq 0.001$ for all cases)

In the worldwide studies of Roberts, and Katzmarzyk and Leonard, Polynesian groups, in particular, are located in anomalous positions on plots of body size and temperature (eg. see Roberts 1953, Figure 7; Katzmarzyk & Leonard 1998, Figures 2, 3, 5 and 6). Although most Polynesians live in the tropics, they are tall and heavy and have body proportions more typical of populations living in temperate climates (Houghton 1996: 60-61). Houghton has theorised that this is due to a high selective pressure on body shape resulting from long distance ocean voyaging (Houghton 1990, 1991, 1996). The Polynesians are great mariners, but their explorations of Oceania often involved long voyages in open outrigger canoes. Houghton demonstrated that this exposed them to hypothermic conditions produced by a combination of wind and water spray, even when sailing in the tropical latitudes (Houghton 1996: 61-63). This, he argued, would have created the situation of high selective pressure, and this combined with relatively small, founding populations must have caused the apparently rapid evolution in body morphology seen in Polynesian groups.

3.3.4.3.2 Clinal and statistical studies on regional population samples

Americas

Both Roberts and Walter examined body/climate relationships in regional populations. For their Native American groups, Roberts found that there was an inverse, but non-significant, relationship between temperature and weight (Roberts 1953, 1973) and Walter (1976) found a relatively weak, but significant, inverse relationships between temperature and stature, and temperature and weight (see table 3.5, above).

Another influential figure in the field of ecogeographic studies was Marshall T. Newman. During the 1950s, he examined evidence for ecogeographic adaptations focusing on the Americas. His approach, however, was perhaps more holistic and, like Walter, he was to come to very different conclusions than Roberts. In his 1953 paper, Newman examined clines of stature, sitting height and various cranio-facial measurements in northern and southern Native American, and Inuit populations. He found that low stature was concentrated around the equator with "irregular increases toward the north and south" (Newman 1953: 325). The stature of the Inuit sample was shorter than predicted, but this was attributed mainly to their shorter leg length (Newman 1953: 325). Clines for other measurements relating to body size (head size and face size) were similar to those of stature (Newman 1953: 325). In this paper Newman proposed that although human populations seemed to follow Bergmann's and Allen's rules and some climatic adaptation was apparent (eg in the Inuit), the relationship between body weight and stature and temperature was likely to be complicated by other environmental factors such as nutrition, altitude, disease and workload (Newman 1953: 319).

His nutritional thesis was developed over several subsequent papers (Newman 1956, 1960, 1975). In his article of 1960, he still argued that climate was responsible for some of variation in body size and shape (Newman 1960: 308). Using 60 Inuit and Native American samples he found a very highly significant correlation between weight and coldest month ($r = -0.729$), meaning that 50% of variation in weight was explained by variation in temperature. He also found in his multiple correlation analysis, 80% of the variation in weight was explained by stature and temperature, with 20% explained by other factors (Newman 1960: 308).

By 1975, however, he had clearly changed his position, arguing that much of the variation in human body size (weight and stature) was due to nutritional differences between populations, in particular to their access to high quality protein. To emphasise his point, he plotted the average daily calorie intake against average body weight for a number of population groups from South America and Asia (reproduced in Figure 3.6 below). He maintained that humans evolved to access high quality proteins containing essential amino acids from animal sources (Newman 1975: 211-214) and that any shortage of this protein (as well as other essential micro-nutrients) to either mother or infant (pre-

and/or post-natally) could lead to deficits in growth (Newman 1975: 224. Thus he argued that:

"the explanation for the remarkably close correlation between mean adult body weights of native peoples and mean annual temperatures of their locations lies less in the body heat retention-dissipation principle and more in the food consumed" (Newman 1975: 240).

He was less certain that body proportions were affected by short-term environmental insults (Newman 1960: 244) stating although there tend to be allometric consequences of body size changes that "generally, body size is considerably more ecosensitive than body proportions" (Newman 1960: 251).

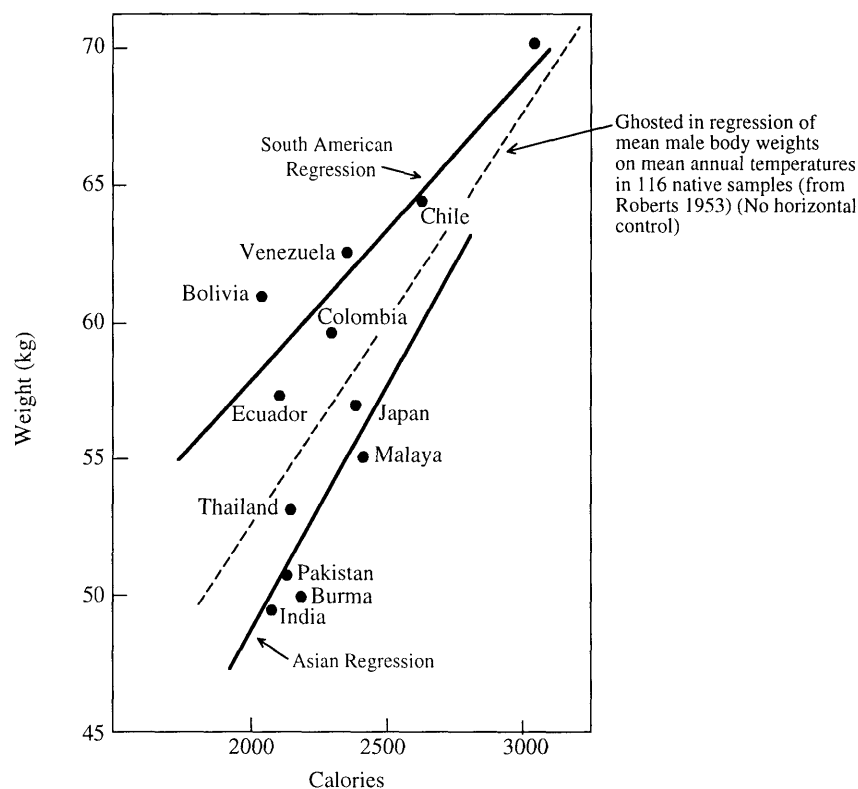


Figure 3.6: Correlation between Weight and Calories in populations from South America and Asia, after Newman, 1975: 241.

For South American native populations Sara Stinson's (1990) study is the most comprehensive published thus far. This study comprised of 62 groups, male and female, spanning a wide area of South America. Most of the correlations, however, were based on much smaller sample sizes, which tends to lessen the strength of her results. The study used the anthropometric variables of height, weight, sitting height and relative sitting height. These were correlated with latitude, longitude, mean annual temperature, temperature of the hottest month, temperature of the coldest month, temperature range, mean precipitation, precipitation of the wettest month, precipitation of the driest month

and precipitation range. The statistic used to calculate the correlation between variables was the non-parametric statistic Kendall's Tau, as Stinson was concerned about the non-normal distribution of some of the variables. The correlations for all but longitude are reproduced in Table 3.8.

Table 3.8: Summary of Kendall's Tau statistics between metrical variables of body size and shape, and location and climate variables in South American males and females, adapted from Stinson, 1990: 44, Table 4.

Variable	Abs Lat	Mean Temp	Hot Temp	Cold Temp	Temp Range	Mean Precip	Wet Precip	Dry Precip	Precip Range
Males									
Stature	0.38**	-0.12	-0.04	-0.16	0.35**	-0.35**	-0.36**	-0.33**	-0.31**
(N)	(62)	(41)	(41)	(41)	(41)	(48)	(48)	(48)	(48)
Weight	0.14	0.12	-0.03	0.01	0.12	0.04	-0.07	-0.16	-0.01
(N)	(20)	(13)	(13)	(13)	(13)	(17)	(17)	(17)	(17)
Sitting Height	0.34**	-0.33*	-0.30	-0.39*	0.35*	-0.43**	-0.40**	-0.31*	-0.38*
(N)	(31)	(22)	(22)	(22)	(22)	(24)	(24)	(24)	(24)
Rel Sit Height	0.02	-0.38*	-0.52**	-0.39*	-0.06	-0.32*	-0.29	-0.08	-0.29
(N)	(29)	(20)	(20)	(20)	(20)	(22)	(22)	(22)	(22)
Females									
Stature	0.38**	-0.08	0.01	-0.21	0.46**	-0.34*	-0.39**	-0.31*	-0.36*
(N)	(34)	(23)	(23)	(23)	(23)	(26)	(26)	(26)	(26)
Weight	0.43*	-0.28	-0.60*	-0.46	0.39	-0.15	-0.24	-0.33	-0.07
(N)	(16)	(10)	(10)	(10)	(10)	(13)	(13)	(13)	(13)
Sitting Height	0.36*	-0.30	-0.25	-0.41*	0.27	-0.48**	-0.57**	-0.30	-0.44*
(N)	(21)	(15)	(15)	(15)	(15)	(17)	(17)	(17)	(17)
Rel Sit Height	0.05	-0.41	-0.49*	-0.38	-0.01	-0.15	-0.25	0.02	-0.24
(N)	(19)	(13)	(13)	(13)	(13)	(15)	(15)	(15)	(15)

(* p significant at 5%, ** p significant at 1% or greater.)

Stinson found that stature increased from north to south and was significantly correlated with rainfall, but not with most temperature variables, apart from temperature range. Thus she found that people tended to be shorter where it was wetter (Stinson 1990: 43-45). Only in the female sample was weight significantly correlated with location or climate: in this case a negative correlation with temperature of the hottest month and a positive correlation with latitude (Stinson 1990: 44). Sitting height was negatively correlated with both rainfall and temperature (the exception again being with temperature range). Correlations between sitting height and rainfall showed a pattern similar to stature, however unlike stature, sitting height manifested significant correlations with temperature. The strong negative correlation with coldest month demonstrated that in hotter areas, sitting height became smaller (Stinson 1990: 45). The fact that sitting height, but not overall stature, increased with decreasing temperature is seen in the correlations for relative sitting height which correlated inversely with temperature as predicted by Allen's rule (eg shorter legs/longer bodies in colder areas) (Stinson 1990: 45). Stinson also found that altitude had a significant effect on the

correlations, with sitting height losing some of its significant correlations among lowland groups (Stinson 1990: 45). Overall it was found that stature was more strongly related to precipitation, and relative sitting height to temperature (Stinson 1990: 46).

Stinson reasoned the absence of significant correlations between stature and temperature variables was due to a lack of samples taken from areas of severe cold. However, this ignores the results from previous studies (reviewed herein) that weight is the more appropriate proxy for body size than is stature in studies of this kind. Stinson's results would suggest that temperature has affected the body proportions of her sample groups (confirming Allen's rule), but the results on body size are less convincing, with a combination of temperature and humidity being implicated. What is interesting is the clear difference in the ecogeographic patterning of male and female body weight.

Ecogeographic rules have also been examined among non-indigenous groups in the Americas. In 1955 Russell Newman and Ella Munro examined the relationship between body size and temperature using a series of 15,216 native-born white American males. The data were collected from army recruits over an eight-year period. The authors tested Schreider's hypothesis that clines in weight to surface area ratio were linked to thermoregulation. They were also interested in identifying which was the major climatic stressor, heat or cold, arguing that modern-day European Americans had the ability to shield themselves adequately from cold weather, but could do little to ameliorate the heat of summer (Newman and Munro 1955: 5).

Their analysis used the climatic variables of mean annual temperature, July (summer) noon effective temperature, mean July temperature and mean January (winter) temperature. They found negative correlations between the climate variables and weight, body surface area, and weight to surface area ratio, with the highest correlation being with winter temperature. Stature was found not to correlate significantly with temperature. Their results are reproduced in Table 3.9.

Table 3.9: Summary of correlations between metrical variables of body size and shape and temperature variables in American white males, adapted from Newman and Munro, 1955: 7.

Variables	Mean Annual Temperature	July Noon "Effective" Temperature	Mean July Temperature	Mean January Temperature
Weight (W)	-0.46**	-0.32*	-0.31*	-0.53**
Stature	-0.04	0.04	0.01	-0.11
Surface area (SA)	-0.36*	-0.22	-0.22	-0.44**
W/SA	-0.54**	-0.40**	-0.38**	-0.59**

(* p significant at 5%, ** p significant at 1% or greater.)

The authors discuss a number of possibilities to explain their results, including uneven sampling with regard to factors of ethnicity and socio-economic status, but ultimately they contend that cold temperatures stimulate appetite and activity and:

"the combination of expanded appetite and muscular activity in the proper proportions results in an actual increase in the quantity of muscular tissue (proteins and associated fluids) and perhaps bone. If an adequate diet is available throughout the period of growth, it is reasonable to suppose that larger body weights and therefore higher weight-surface area ratios will be found in areas with either a more severe cold stress, or one of longer duration" (Newman and Munro 1955: 12).

Sub-Saharan Africa

In his 1953 and 1973 papers, Roberts reported an inverse, but not particularly strong, relationship between body size and temperature, and a direct relationship between relative limb length and temperature in his African sample. The weak correlation between weight and temperature he attributed to the absence of very cold climates in sub-Saharan Africa. In contrast Walter (1976) was to find no significant relationship between temperature and weight in his African sample. He did, however, find a low but significant, positive relationship between temperature and stature (see Table 3.5, above).

The scientist who has most thoroughly examined ecogeographic correlations in sub-Saharan Africa is Jean Hiernaux (Froment & Hiernaux 1984; Hiernaux 1968, 1974, Hiernaux & Froment 1976). Hiernaux's main interest lay in the phylogenetic relationship between sub-Saharan African groups and in order to sort out their interrelationships he had to account for adaptation to environment (climate, nutrition and disease) and population movement. In his 1968 monograph *La Diversité Humaine en Afrique Subsaharienne*, he collected together data of 16 anthropometric measurements and 2 indices from some 460 populations. These measurements covered the head, face and body, but only the last is reviewed in this section, with those of the face and head discussed below in sections 3.3.4.4.2 and 3.3.4.4.3. Hiernaux measured some of these data personally, but many of the samples were taken from other studies. As a result not all measurements were available for all groups (see Table 3.10 below), and sample size varies between measurements. Hiernaux correlated the majority of his anthropometric variables with one geographic and five climatic variables. These included altitude, log mean annual rainfall, maximum temperature of hottest month, minimum temperature of the coldest month and the humidity mixing ratios of the most humid and least humid months. He also correlated a subset of variables with annual ranges in temperature and humidity. Hiernaux stated that these climatic variables were chosen as representing the periods of maximum climatic stress on humans.

His results, compiled from Hiernaux (1968: 69-78; 83) and Hiernaux and Froment (1976: 760-761, Table 1), are summarised in Table 3.10. Hiernaux found that stature was directly related to temperature (contra Bergmann) but inversely related to humidity. Thus the tallest Africans among his sample groups were found in hot and relatively dry areas. In particular, he found tall stature in areas of climatic extremes (with large ranges

annual in temperature and humidity) and smaller stature in areas of climatic uniformity (Hiernaux 1968: 69). There was also a low but significant inverse relationship between stature and log rainfall (ie. shorter people in wetter areas). The highest correlation for stature was $r = 0.48$ with humidity range, followed by $r = 0.45$ with maximum temperature. Both correlations are highly significant, however they explain only about 20% of variation in stature.

There were no significant correlations between weight and any of the climatic variables and the only significant coefficient was a negative one with altitude. When variation in stature was accounted for in the partial correlations, Hiernaux found that very little changed except that a significant positive correlation between weight and log rainfall emerged (Hiernaux 1968: 70).

Sitting height demonstrated a somewhat different pattern to stature, failing to achieve a significant correlation with log rainfall, and gaining a low, but significant correlation with minimum temperature. However, with stature accounted for, the situation was reversed (Hiernaux 1968: 71). Hiernaux concluded that in the more humid areas people tended to have relatively longer trunks and in dry areas relatively longer legs (Hiernaux 1968: 71).

Table 3.10: Summary of correlations between anthropometric measurements of the body, and location and climate variables in sub-Saharan African males, adapted from Hiernaux, 1968 and Hiernaux and Froment, 1976.

Variable	N	Log Rain	Humid max	Humid min	Temp max	Temp min	Altitude	Humid range	Temp range
Stature	312	-0.26**	0.15**	-0.35**	0.45**	0.06	-0.21**	0.48**	0.30**
†	330	-0.26**	0.13*	-0.35**	0.44**	0.05			
Weight	63	-0.09	0.20	-0.07	0.19	0.11	-0.27*		
†	78	-0.02	0.12	-0.14	0.25*	0.08			
Sitting Ht	87	-0.18	0.40**	-0.40**	0.57**	0.33**	-0.48**		
†	107	-0.13	0.35**	-0.32**	0.50**	0.31**			
Arm Lgth	58	-0.25	0.05	-0.38**	0.39**	0.14	-0.22		
†	67	-0.24	0.06	-0.41**	0.38*	0.15			
Biacromial	106	0.55**	0.19	0.07	0.02	0.36**	-0.30**		
†	126	0.45**	0.16	0.02	0.04	0.31**			
Bi-iliac	62	-0.35**	0.14	0.01	0.21	0.15	-0.11		
†	81	-0.43**	-0.04	-0.14	0.15	-0.04			
Chest W	37	-0.50**	-0.24	-0.33*	0.24	-0.21	-0.04		
†	44	-0.44**	-0.24	-0.29	0.07	-0.26			
Chest D	36	0.000	-0.02	-0.12	0.04	-0.18	0.10		
†	43	-0.10	-0.13	-0.12	-0.08	-0.14			
Calf Circ	32	0.27	0.38*	0.13	0.01	0.19	-0.20		
†	41	0.09	0.17	0.02	0.03	0.18			

(* p significant at 5% level; ** p significant at 1% level; † sample sizes and correlation coefficients from Hiernaux and Froment (1976). Values in bold type indicate significant differences in results between studies.)

Of the other body variables examined, absolute arm length was found to be longer in the hot, dry areas, however Hiernaux felt that this was due to arm length's correlation with stature (Hiernaux 1968: 71-72). The correlations of biacromial and bi-iliac diameters indicated that populations in drier areas tended to have narrower shoulders and wider hips, and in more humid areas, broader shoulders and narrower hips (Hiernaux 1968: 72-

73). Interestingly, chest width was found to produce the same pattern of correlations as bi-iliac breadth, with narrower chests found in wetter areas (Hiernaux 1968: 73). Chest depth on the other hand showed no significant correlations (Hiernaux 1968: 73). Calf circumference had only one significant correlation with maximum humidity indicating that populations living in the more humid areas of sub-Saharan Africa exhibited thicker calves (Hiernaux 1968: 73-74).

Hiernaux concluded in his 1968 paper that neither Bergmann's nor Allen's rules applied to humans in sub-Saharan Africa. He argued that either Bergmann's rule only operated at a certain threshold and in Sub-Saharan Africa it is not cold enough to reach this threshold, or that the rule was not universal and African populations had a different way of maintaining thermal homeostasis (Hiernaux 1968: 89). He also noted that in Africa humidity appeared to be a more influential factor than temperature in the ecogeographic patterning of human body morphology.

Hiernaux argued that variation in weight was primarily associated with nutrition levels, and that weight's association with rainfall was probably due to the relationship between rainfall and agricultural production (Hiernaux 1968: 89). He emphasised that the correlations did not necessarily represent direct relationships between his variables and that they were likely to be multifactorial in nature:

"Il est probable que chacun des coefficients de corrélation calculés représente la composante de plusieurs processus ou situations, parmi lesquels la sélection, la dérive génique, la parenté phylogénétique et éventuellement l'association entre milieu et type d'activité." (Hiernaux 1968: 85)

"It is likely that each correlation coefficient represents the combination of many processes or events, including selection, genetic drift, phylogenetic relationships and possibly the association between environment and activity type." [Author's free translation]

In 1976, Hiernaux working with Froment, added some extra groups to the database (see Table 3.10 above). Few correlations were changed by the addition of these groups and thus the authors argued for the stability, and thus validity, of the original correlations. The few changes that did occur involved weight (the positive correlation with maximum temperature became significant), chest width (lost its significant correlation with minimum humidity) and calf circumference, which lost its one significant correlation (Hiernaux & Froment 1976: 759-762).

In this paper Hiernaux's conclusion that Allen's rule did not operate in sub-Saharan Africa was revised. Hiernaux and Froment argued that a tall, linear form is adaptive to the hot, dry and open environments (eg. the savanna) because it maximises body surface area to body mass, allowing more efficient evaporative cooling of the body (Hiernaux & Froment 1976: 765). Accounting for the short stature of the pygmy peoples, they

contended that in the humid forest the evaporative method of thermoregulation was inefficient and this may have led to a reduction of body size which also acted to increase the ratio between surface area and mass. The authors argue that the apparent lack of evidence supporting Bergmann's rule is due to the fact that in Africa "body size responds mainly to climatic factors which are not included in its formulation", in particular to factors of moisture (Hiernaux & Froment 1976: 765). They went on to argue that these adaptations were likely to be due to the direct influence of climate and were essentially genetic in nature (Hiernaux & Froment 1976: 766). These conclusions were supported by the results of a more regionally defined study by Froment and Hiernaux examining human variation in populations in the Niger bend region of West Africa (Froment and Hiernaux 1984).

Europe and the Mediterranean

In his European sample, Roberts found a clear negative, and significant, relationship between weight and temperature (Roberts 1953, 1973) and in Walter's study, both stature and weight manifested negative and significant relationships with temperature (Walter 1976). Apart from Roberts and Walter, the only person to examine ecogeographic correlations in Europe and the Mediterranean was Crognier (1981a, 1981b). Fourteen anthropometric measurements were collected from a sample of 85 male and 35 female European, North African and Middle Eastern groups. These were correlated with 8 climatic variables. His statistical methodology included zero order correlation, multiple stepwise regression and a comparison of 3 distance matrices based on anthropometric measurements, climate and geographic distance. His results for the first two analyses are summarised in Tables 3.11 and 3.12 below.

Table 3.11: Summary of correlations between anthropometric measurements and climate variables in European, Middle Eastern and North African males, adapted from Crognier, 1981b: 102.

Variables	n	Mean annual temp	Mean temp cold month	Mean temp hot month	Mean annual temp range	Mean annual rainfall	Mean rainfall wet month	Mean rainfall dry month	Mean altitude
Stature	85	-0.277**	-0.050	-0.370**	-0.293**	0.340**	0.182	0.335**	0.030
Weight	27	-0.706**	-0.460*	-0.722**	-0.312	0.518**	0.332	0.764**	-0.012
Sit Height	38	-0.190	-0.051	-0.123	-0.137	-0.290	0.185	0.390*	0.084
Biiliac D	26	-0.614**	-0.623**	-0.629**	0.294	0.641**	0.461*	0.433*	0.217
Biac D	29	-0.447*	-0.347	-0.482**	0.093	0.386*	0.326	0.355	0.140

(* p significant at 5%, ** p significant at 1% or greater.)

Table 3.12: Results of a multiple stepwise regression analysis between anthropometric measurements and climate variables in European, Middle Eastern and North African males, adapted from Crognier, 1981b: 104.

Variables	n	Mean annual temp	Mean temp cold month	Mean temp hot month	Mean annual temp range	Mean annual rainfall	Mean rainfall wet month	Mean rainfall dry month	Mean altitude
% contribution to the analysis									
Stature	85	5.68	1.97	13.67	11.27	-	-	-	-
Weight	27	-	-	-	4.07	-	-	58.34	-
Sit Height	38	-	-	2.62	-	2.74	-	15.21	-
Biiliac D	26	-	13.52	-	-	41.1	-	-	-
Biac D	29	-	-	23.27	-	-	-	-	1.48

(* p significant at 5%, ** p significant at 1% or greater.)

Table 3.13: Summary of correlations between anthropometric measurements and climate variables in European, Middle Eastern and North African females, adapted from Crognier, 1981a: 613.

Variable	n	Mean annual temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
Stature	34	-0.38*	-0.12	-0.27	-0.25	0.26	0.24	0.42*	-0.06

(* p significant at 5%, ** p significant at 1% or greater.)

The results of his correlation study indicate that stature produced low but significant negative correlations with mean annual temperature, mean temperature of the hottest month and mean annual temperature range. It also had low but significant positive correlations with mean annual rainfall and mean rainfall of the driest month. These results are mirrored in his female sample where stature was the only variable tested (Table 3.13). In the male sample, meanwhile, weight produced a similar pattern of correlations to stature, but overall the correlations were stronger.

Of the other variables examined, sitting height has a low but significant positive correlation with mean rainfall of driest month. Bi-iliac diameter has moderate and negative significant correlations with temperature variables, and positive correlations with rainfall. Therefore the tallest, heaviest and stockiest populations are found in cold and or/wet regions and the smallest or leanest are found in the hottest and/or driest regions (Crognier 1981b): 101). Crognier claims that his results support Bergmann's rule (1981b: 103), however he also warns that because of inter-correlations among his climate variables, that some of the correlations between climate and anthropometrical measurements may be spurious (Crognier 1981b: 103). In an attempt to overcome this problem he used stepwise regression. The results of this analysis (Table 3.12) tend to show that the:

"previously observed major importance of peaks of heat and dryness on body size and shape is confirmed ... Postcephalic features are essentially correlated either with the mean temperature of the hottest month (which accounts for 13.7% of the variance of standing height and for 23.3% of the variance of biacromial breadth) or with the mean precipitation of the driest month (58.3% of the variance of weight and 15.2% of that of sitting height).

The biiliac breadth alone shows different dependence, for its 41% variance with the mean annual precipitation and 13.5% in relation to the mean temperature of the coldest month." (Crognier 1981b: 104).

Crognier accounted for the puzzling fact that cold did not seem to be an important stress factor in a predominantly temperate region, by postulating that cultural buffering protects better from cold than from heat (Crognier 1981b: 105).

In Crognier's other paper (Crognier 1981a) he compared three distance matrices generated from a sub-set of 43 male groups using sets of: 1) anthropometric variables (stature, sitting height, biiliac diameter, cephalic index and nasal index); 2) climate variables (hottest month, annual temperature, temperature range, driest month, wettest month) and 3) geographic distance. He then calculated the pairwise correlation coefficients between each set of distances. He found that " r " anthropometric vs geographic = 0.252, " r " anthropometric vs climatic = 0.412 and r climatic v geographic = 0.400 with all coefficients significant at 0.01 (Crognier 1981a: 613). When geographic distances were accounted for in a partial correlation a significant relationship of $r = 0.351$ was revealed to exist between the biometric and climate distances. From this Crognier concluded that up to 17% of the physical variation in his study region resulted from differences in climate (Crognier 1981a: 614).

Asia

Apart from worldwide studies of Roberts and Walter little research into ecogeographic correlation has been done for the Asian region. Roberts found a significant negative correlation between weight and temperature within his Asian sample (Roberts 1953, 1973) and Walter found negative and significant relationships between weight, stature and temperature (Walter 1976). Ruff has also reported a very strong positive correlation between bi-iliac breadth and latitude of $r = 0.956^{***}$ for his East Asian pooled male and female sample (Ruff 1991: 86).

One notable study of ecogeographic correlations in an Asian population is that of Endo et al. (Endo *et al.* 1993). Using prefectural data collected over 35 years, the authors examined the relationship between body size and environment in 17-year-old Japanese. Correlation analysis revealed an inverse relationship between mean annual temperature and the body size variables of height and weight (Endo *et al.* 1993: 299-300). Partial correlation analysis found that body weight was primarily correlated with temperature, however when annual income was included in a multiple correlation analysis, the authors found that the apparent conformation with Bergmann's rule was more likely to be related to geographical differences in nutrition, with individuals in colder regions consuming more calories than those in warmer regions (Endo *et al.* 1993: 302). In this, their conclusions mirror those of Walter (1976) and Newman and Munro (1955).

Australia

Whilst Birdsell had examined the possibility that climate had influenced the geographical distribution of body morphology in Aboriginal Australians (Birdsell 1993), his analysis was perfunctory (see section 3.22). The only published study to specifically examine ecogeographic correlation within Aboriginal populations was that of Macho and Freedman (1987). Roberts (1953, 1973) did include a very small sample of Australians in his studies and Walter (1976) included an "*Australide*" group that seems to correspond with an Austro-Melanesian grouping and is thus not directly comparable to Macho and Freedman's study. There is also an unpublished thesis produced on the subject by Sheila van Holst Pellekann, but this deals with cranio-facial variation and will be discussed in section 3.3.4.4.2.

Macho and Freedman used Andrew Abbie's anthropometric data that were collected from a broad transect through the centre of Australia (Abbie 1975). In their analysis the authors utilised 17 head and 14 body variables (see Tables 3.14 and 3.15 below) and the climate variables of median rainfall of the hottest month (January), maximum average temperature of the hottest month, minimum average temperature of the coldest month (July), temperature range of the coldest month, mean relative humidity of the hottest month and mean relative humidity of the coldest month (Macho & Freedman 1987: 32-34).

As Macho and Freedman only published the results of the step-wise multiple regression analysis, that reveals the degree but not the direction of covariation, it is hard to compare their results with those of most other studies, apart from that of Crognier (1981a, 1981b). They found that weight and sitting height did not correlate significantly with any climate variables, however stature, radius length and measurements of the hand did, particularly so with temperature range of the coldest month. Further, 10.4% of variance in female radius length was explained by variance in minimum winter temperature (July) and variation in the length of the upper arm could also be explained by variation in climate, with summer rainfall correlating with humerus length in both males and females. When body indices were examined it was found that in males ponderal index covaried with all temperature variables, and relative sitting height shared variance with temperature range of the coldest month (Macho & Freedman 1987: 47). The situation was somewhat different in the female sample, however with relative sitting height correlating with temperature extremes and to a lesser degree with winter humidity. Relative humidity of the hottest month explained 10.11% of variance in tibia length in males, and minimum temperature of the coldest month explained only 3.77% of variance in femur length in females. Given the pattern of correlations with regard to weight, stature, sitting height and their related indices, the authors conclude that it is variation in the lower limb that seems to "underlay the influence of climate on stature" (Macho & Freedman 1987: 53). This is interesting considering that neither femur nor tibia length share variance, either strongly or consistently, with climate variables used in their study.

Their overall conclusion was that temperature range of the coldest month appeared to have the greatest influence over Aboriginal body morphology, but that it was uncertain as to how much of this variation was due to genetic differences or plasticity (Macho & Freedman 1987: 53-54).

Table 3.14: Results of a multiple stepwise regression analysis between anthropometric measurements and climate variables in Australian Aboriginal males, adapted from Macho and Freedman, 1987: 44, Table 10.

Variables	% Contributions to the regression analysis						Multiple <i>r</i>
	Rain Jan	Max Temp Jan	Min Temp July	Temp range cold	Hum Jan	Hum July	
Weight	-	-	-	-	-	-	-
Stature	-	-	-	12.12**	-	-	0.35**
Sitting Height	-	-	-	-	-	-	-
Shoulder Br	-	-	-	-	-	-	-
Thoracic Br	-	-	-	-	-	-	-
Thoracic D	-	-	-	-	-	6.32**	0.25**
Bi-iliac Br	2.16**	-	-	-	-	-	0.15*
Humerus L	8.49**	-	-	-	-	-	0.29**
Radius L	4.43**	3.24**	-	4.71**	-	3.78**	0.40**
Hand L	-	-	-	13.90**	-	-	0.37**
Hand B	-	-	-	8.54**	-	-	0.29**
Index Finger L	2.72**	-	-	-	-	-	0.17*
Femur L	-	-	-	-	-	-	-
Tibia L	-	-	-	-	10.11**	-	0.32**
Rel Sit H	-	-	-	10.52**	-	-	0.32**
Ponderal Index	-	1.83**	2.38**	12.08**	-	-	0.40**

(* $p \leq 5\%$; ** $p \leq 1\%$; blank cells indicate non-significant results)

Table 3.15: Results of a multiple stepwise regression analysis between anthropometric measurements and climate variables in Australian Aboriginal females, adapted from Macho and Freedman, 1987: 45, Table 11.

Variables	% Contributions to the regression analysis						Multiple <i>r</i>
	Rain Jan	Max Temp Jan	Min Temp July	Temp range cold	Hum Jan	Hum July	
Weight	-	-	-	-	-	-	-
Stature	-	-	-	10.28**	-	-	0.32**
Sitting Height	-	-	-	-	-	-	-
Shoulder Br	13.15**	-	-	-	-	-	0.36**
Thoracic Br	-	-	3.90**	-	-	-	0.20*
Thoracic D	-	-	-	-	-	-	-
Bi-iliac Br	-	-	-	3.51**	-	-	0.19*
Humerus L	5.75**	-	-	-	-	-	0.24**
Radius L	-	2.77**	10.39**	6.25**	-	4.07**	0.48**
Hand L	-	-	-	14.24**	-	-	0.38**
Hand B	-	-	-	9.17**	2.49**	6.28**	0.42**
Index Finger L	-	-	-	-	-	-	-
Femur L	-	-	3.77**	-	-	-	0.19*
Tibia L	-	-	-	-	-	-	-
Rel Sit H	-	7.69**	6.86**	-	-	3.52**	0.43**
Ponderal Index	-	-	-	11.13**	-	-	0.33**

(* $p \leq 5\%$; ** $p \leq 1\%$; blank cells indicate non-significant results)

3.3.4.4 Ecogeographic Studies: Head and Face

3.3.4.4.1 Introduction

In terms of human studies, one of the earliest areas of ecogeographic research was the relationship between climate and craniofacial morphology, and in particular the shape of the nose. Studies began early in the 20th Century and were spurred on by the theory that features such as nasal shape were "racial" traits. But a number of authors were to challenge this assumption, arguing that the nose was unlikely to be selectively neutral given its important respiratory function. Other researchers, such as Coon and his collaborators went on to argue that the whole human face was subject to climatic selection and this spawned numerous studies testing their hypothesis. The last skeletally based sacred cow of racial typology to be challenged was the Cephalic or Cranial Index. Beals and his coworkers were to find evidence that even the shape of the cranium itself was under climatic selection.

3.3.4.4.2 Ecogeographic studies of nasal and facial shape

Conceptual studies, and studies using worldwide samples

It was Thomson and Buxton (Thomson 1913; Thomson & Buxton 1923) and later Davies (Davies 1932), who initiated research into the relationship between climate and cranio-facial morphology. Their particular interest was in nasal shape as estimated by the nasal index (nasal breadth/nasal height*100)(NI hereafter). As Davies notes, anthropologists such as Deniker (1889), Dixon (1923), Haddon (1925) and Hrdlicka, identified NI as one of the major defining features of their racial typologies (Davies 1932: 337 and references therein). Thus studies that examined the nature of nasal adaptation to environment were important to the debate over the causes of modern human variation, and to the very existence of race.

Arthur Thomson first raised this issue in 1913, and following World War 1 published a second paper in 1923 with Dudley Buxton. In the earlier paper Thomson found that in Native Americans, average nose breadth was greater in populations living closer to the equator (Thomson 1913). In the second paper, the authors used product moment correlation analysis to examine the relationship between nose shape and climate on living and skeletal worldwide samples. The authors found that a positive relationship existed between temperature and humidity and NI. Temperature was found to be the major contributor to the observed variation, with relative humidity having a lesser, secondary effect (Thomson and Buxton 1923): 107). They reported correlations between NI and mean annual temperature of $r = 0.6291$, and between NI and mean annual relative humidity, $r = 0.4188$. Apparently using multiple correlation (the authors do not clearly state their methodology) they found that variation in temperature and relative humidity explained about 52% of variation in nasal index (r NI vs temperature and relative

humidity = 0.7238) (Thomson and Buxton 1923: 104-105). Their results indicated that more platyrrhine (relatively wide) noses were found in areas of high temperature and/or humidity and that leptorrhine (relatively narrow) noses were found in cold and/or dry regions. They related this finding to the respiratory function of the nose and the requirement of the lungs for air of a particular temperature and moisture content. In areas where the air is cold or dry, the internal surfaces of the nose help to warm and moisten inspired air (Thomson & Buxton 1923: 94). Meanwhile, in hot, humid climates, a broad nose may help the body lose heat where sweating is inefficient and/or help to regain moisture lost from the lungs during expiration (Thomson and Buxton 1923: 99). From their results the authors put forward the hypothesis that the nasal index, long seen as an indicator of ethnic origin, actually owed its shape to the climatic conditions under which a particular population lived (Thomson and Buxton 1923: 112).

Davies followed up on Thomson and Buxton's work in his paper of 1932. He used a much larger series of samples ($n = 652$, living and $n = 160$ skeletal), and apparently (the methodology is not made clear) correlated NI with the maximum mean temperature combined with relative humidity of a "typical summer month" (Davies 1932: 339). His results are reproduced in Table 3.16.

Table 3.16: Summary of multiple correlations between nasal index (living) and summer temperature and relative humidity, adapted from Davies, 1932.

Region	<i>r</i>
World	0.60
World (except India)	0.71
Africa	0.81
Europe	0.77
North and South America	0.68

Davies' results clearly mirror those of the previous studies and he attributes them to the same causes. However, he argued that it was summer temperature that exerted the most influence over nose shape, and that winter temperature had little effect (Davies 1932: 344). Exceptions to the rule, he maintained, were due to recent migrations, an overspecialised nasal shape, or isolation, inbreeding and/or a "halt of culture at a lowly stage" (Davies 1932: 339; 343). Two other important contributions of his work included the realisation that the relationships between NI and temperature, and NI and humidity, are non-linear, with the rate of change in NI increasing as both temperature and humidity increase (Davies 1932: 345, Figures 1 and 2). Following on from this, is the conclusion that nasal-form adaptation is due to a threshold effect, as the "task of keeping cool becomes increasingly difficult with the rise of temperature and relative humidity" (Davies 1932: 348). The threshold level appeared to be about 78°F (c. 27°C). These are important discoveries, but as Steegmann (1975) has pointed out, neither of these conclusions has been tested further.

In 1954, Weiner revisited Thomson and Buxton's study, and using their "living" sample groups, correlated NI with two further climatic variables: wet bulb temperature and vapour pressure of the air. He argued that Thomson and Buxton had undervalued the importance of their moisture variable due to their use of the relative amount of moisture in the air as measured by relative humidity. Weiner argued that the nose experiences only the absolute amount of moisture in the air, and thus, this was the appropriate variable to use when examining issues of adaptation linked to moisture exchange in the nose (Weiner 1954: 616-617). He found that by correlating nasal index with vapour pressure he achieved a correlation coefficient of $r = 0.82$, almost double that of the correlation between NI and relative humidity (Weiner 1954: 618).

Beals also collected data on the ecogeographic distribution of the Nasal Index in 82 populations and reported a correlation of -0.49^{***} between NI and climate zone (Beals *et al.* 1984: 308). These findings suggested that the broadest and/or shortest noses were to be found in areas of dry heat and the narrowest and/or highest noses in areas of dry cold. This would seem to suggest that temperature rather than humidity had the most influence on nose shape.

The orthodoxy that variation in NI, and thus its relationship to temperature, being based on variation in its width portion was challenged by Hoyme (Hoyme 1965). Hoyme noted that in the cranial series she had measured, variation in NI was due to variation in nasal height, rather than nasal breadth. Thus she argued that Thomson and Buxton's hypothesis that climatic selection worked on nasal breadth could not be sustained. Indeed she concluded that nasal height was closely correlated with upper facial height and any theory regarding climatic selection in nose shape should also include face shape (Hoyme 1965). The conclusion that nasal height was not the direct unit of selection was later supported by Wolpoff's investigation of the issue of nasal adaptation (Wolpoff 1968). Both Wolpoff's and Hoyme's studies highlighted the fact that no one facial feature can be treated in isolation and that a multitude of factors are responsible for variation in cranio-facial morphology (Wolpoff 1968: 421-422). Wolpoff also suggested that NI (height/breadth) is an inappropriate measure of total nasal shape and that a measurement of protrusion should also be included (Wolpoff 1968: 408-411). The specific results Wolpoff's study relates to two regional populations and will be examined in more detail below.

Research into the relationship between nasal and facial protrusion and climate was also conducted by Carey and Steegmann (1981) who correlated 4 indices of facial protrusion with 11 climatic and 2 geographic variables. Their sample was drawn from 55 skeletal groups originally measured by Woo and Morant (1934). Of the anthropometric variables, facial protrusion produced no significant correlations. The variables of relative humidity, diurnal temperature range, and longitude also failed to show any relationship with naso-facial morphology. The significant results are presented in Table 3.17.

Absolute humidity was found to have the strongest correlation with nasal protrusion. The authors state that "...the human nose projects more in dryer areas than in humid ones, and more in cold climates than in warm ones " (Carey & Steegmann 1981: 315). Whilst they confirmed Weiner's results that absolute humidity, not relative humidity or temperature, was the strongest correlate of nose shape, they also found that latitude was second only to absolute humidity in predictive value (Carey & Steegmann 1981: 317).

Table 3.17: Summary of the correlations* between absolute and relative measures of nasal protrusion (skeletal) and climatic and geographic variables, adapted from Carey and Steegmann, 1981: 316, Table 1.

Variables	Absolute protrusion at nasal root	Absolute protrusion of mid-nose	Relative nose protrusion at nasal root	Relative protrusion of distal tip of nasal bones
Latitude	0.65 (46)	0.66 (43)	0.69 (52)	0.68 (49)
Mean temperature of coldest month	-0.58 (49)	-0.58 (46)	-0.64 (55)	-0.58 (52)
Mean temperature of warmest month	-0.34 (49)	-0.41 (46)	-0.48 (55)	-0.39 (52)
Mean absolute humidity of coldest month	-0.72 (43)	-0.72 (40)	-0.61 (49)	-0.63 (46)
Mean absolute humidity of warmest month	-0.70 (43)	-0.68 (40)	-0.52 (49)	-0.53 (46)
Mean absolute humidity of wettest month	-0.72 (43)	-0.71 (40)	-0.52 (49)	-0.52 (46)
Mean absolute humidity of driest month	-0.71 (43)	-0.71 (40)	-0.60 (49)	-0.61 (46)
Mean annual diurnal range in absolute humidity	-0.67 (42)	-0.62 (39)	-0.53 (48)	-0.55 (45)

(n) = sample size; *all correlations significant at 5% level or better.)

A more recent study by Franciscus and Long (1991) has examined the whole issue of climatic selection in Nasal Index. Analysing variance-covariance matrices based on the skeletal nasal height and breadth of 26 mixed-sex populations (n = 2,408), their study supported Thomson's original assertion that it is variation in nasal breadth, not nasal height, that underlies the variation in NI (Franciscus & Long 1991). Like Wolpoff, they also included nasal protrusion as an element of nasal shape, and suggested that multivariate studies of facial shape would be more likely to uncover relationships between climate and facial shape than would univariate or bivariate studies.

The fact that the entire face might be the unit of selection rather than its elements in isolation was suggested as far back as 1950 when Coon, Garn and Birdsell published "Races... A study of the problems of race formation in Man". Among their suggestions was that the some of the facial features typical of modern human groups were the result of adaptations to their habitual environments. For instance, the typical Mongoloid

features of a flat, wide face with a non-protrusive nose were seen as adaptations to extreme cold (Coon, Garn, and Birdsell 1950: 65). In populations living in areas of extreme cold, the face is the only part of body left relatively unprotected by clothing. The authors argued that facial adaptations helped to prevent the loss of body heat by reducing the amount of facial surface area exposed to the cold to a minimum by the "flattening out as much as possible all protuberances" and through "padding the surface with fat" as well as "banking up the nasal passages to provide the maximum heat for the air on its way to the lungs" (Coon, Garn, and Birdsell 1950: 71). The flattening of the face was also thought to prevent frostbite injury.

A comprehensive treatment of the issue of climatic selection and facial morphology has been undertaken by Steegmann. He set out to specifically test Coon's hypothesis of the cold-engineered Mongoloid face. Most of his papers on the subject involve experimentation (Steegmann 1965, 1970, 1972; Steegmann & Platner 1968) and these will be discussed in section 3.3.4.5.3. In his 1967 paper Steegmann reviewed published studies on frost-bite injury and found that "96% to more than 99% of all frostbite injuries occurred to the feet and hands, not to the head and face" (Steegmann 1967: 134). He found that faces of both Europeans and Inuit were subject to low levels of frost-bite injury and that both suffered from greater injury to the hands and feet (Steegmann 1967: 137-138). Further, he noted that in studies on cold injury in the Korean War, people of African ancestry were more susceptible to cold injury than those of European ancestry, but injuries to the faces of both groups were still relatively mild (Steegmann 1967: 138). Given that it appeared that all human faces, not just those of Mongoloids, were relatively resistant to cold injury, Steegmann contended that adaptations to cold and cold injury had primarily been cultural and that physiological and morphological adaptations were of secondary importance and not restricted to the face alone (Steegmann 1967: 140-141).

Regional Studies: the Americas

As mentioned above the earliest study of ecogeographic correlations and cranio-facial shape involved Native American populations, with Thomson finding that nose breadth tended to increase towards the equator (Thomson 1913). Forty years later, Newman (1953) examined facial proportions in the Americas, and found that in Native Americans, faces and noses became relatively longer and narrower with increasing latitude in both North and South America (Newman 1953: 325). However, he concluded that whilst the clines in facial and nasal proportions could not be directly linked to either Bergmann's or Allen's rules, they were "in all likelihood ... due to the same factors of temperature and humidity." (Newman 1953: 319). From this he concluded that the use of traits such as nose shape to define the racial origins of the first inhabitants of the Americas was "erroneous" (Newman 1953: 325).

As a result of Coon's hypothesis concerning the cold engineering of the Mongoloid, or Arctic, face, many studies have concerned the Inuit peoples of North America. In 1968

Wolpoff examined craniofacial variables in a large number of male ($n = 213$) and female ($n = 268$) Inuit crania. The crania were grouped into three regional samples that differed in geographic location and climatic conditions. Unlike many other ecogeographic studies his methodology utilises univariate comparisons of the variables. Wolpoff hypothesised that noses should become higher and narrower as average temperature and humidity decreased (Wolpoff 1968: 418-419). He found support for his hypothesis with his results demonstrating that nasal breadth decreased from south to north, and this reduction was real and unassociated with palatal and facial breadth which, in contradistinction, increased south to north. Measures of nasal and facial height did not appear to have any relationship with climate, however measures of palate and cranial base length (which are also measures of sagittal face depth) were inversely related to temperature: a situation linked perhaps to an increase in facial and/or nasal protrusion in colder areas (Wolpoff 1968: 418) (see also Carey & Steegmann 1981).

In order to investigate whether interior nasal shape and volume were the actual units of selection by climate, Shea examined the maxillary sinus volume of 362 adult Inuit crania (Shea 1977). These were compared to one Mongoloid and one European group. Based on the location of the maxillary sinus lateral to nasal cavity, Shea hypothesised that any increase in the volume of the nose in order to add extra surface area for the warming of inspired air would "encroach on the capacity of the maxillary sinus" (Shea 1977: 295), and thus in colder areas this sinus should become smaller as nose volume increased. He reported significant correlations between mean temperature of the coldest month and maxillary sinus volume of $r = 0.82$ for males and $r = 0.79$ for females (Shea 1977: 291). His correlations between sinus volume and absolute humidity were not significant. Shea found that his hypothesis was confirmed, and argued that the Inuit peoples had evolved a "highly efficient 'air conditioning' system ... characterised by restricted nasal aperture width, but an appreciably expanded internal nasal chamber, with enlarged conchae, meatuses, etc" (Shea 1977: 298).

Little work on ecogeographic correlations of the face has been conducted on South American populations alone. Rothhammer and Silva (1990) examined the role of climate and geography in the cranio-facial variation of 25 groups ($n = 1,119$). Using least squares multiple regression they found that climate had only a "modest" effect on cranio-facial variation and that the stochastic factors of geographic isolation and founder effect were more influential (Rothhammer & Silva 1990: 16).

Africa

Hiernaux has produced what would appear to be the only major study (if not the only study) of ecogeographic correlations in cranio-facial variables for sub-Saharan African populations. His results and those of Hiernaux and Froment (1976) are reproduced in Table 3.18. His results are somewhat at odds with those of other studies, with neither temperature nor humidity strongly correlating with nasal shape.

Table 3.18: Summary of correlations between anthropometric measurements of the face, and location and climate variables in sub-Saharan African males, adapted from Hiernaux, 1968, and Hiernaux and Froment, 1976.

Variables	N	LnRain	Hum+	Hum-	Temp+	Temp-	Alt	Hum range	Temp range
Bizyg	160	0.41**	0.21**	0.31**	-0.21*	0.26**	-0.04	-0.22**	-0.39**
†	185	0.34**	0.19**	0.27**	-0.15*	0.24**			
Tot Fac H	86	-0.05	0.06	0.06	-0.20	-0.12	0.29**		
†	112	-0.13	-0.07	-0.05	-0.21*	-0.18			
Nasal H	105	-0.16	-0.26**	-0.15	-0.11	-0.21*	0.37**		
†	131	-0.22**	-0.32**	-0.20*	-0.18*	-0.27**			
Nasal B	179	0.49**	0.05	0.10	-0.33**	0.00	0.05		
†	203	0.42**	0.02	0.08	-0.35**	-0.03			
Facial I	108	-0.39**	-0.20*	-0.27**	0.08	-0.25**	0.27**		
Nasal I	123	0.46**	0.25**	0.28**	-0.21*	0.22*	-0.23**	-0.12	-0.34**

(* 5%; ** 1%; † sample sizes and correlation coefficients as in Hiernaux and Froment, 1976: 760-761, Table 1. Bold type indicates where significant differences between the two studies exist.)

The results of most other studies have suggested that noses get higher and narrower as temperature and/or humidity declines. Whilst Hiernaux's results do indicate that nasal height in sub-Saharan populations is inversely related to temperature and humidity the correlations are not particularly strong. Nasal height has its highest correlation with altitude (positive and significant) and this persists even when the variables of humidity and temperature are partialled out. Nasal breadth has a positive correlation with log rainfall, and a negative correlation with temperature of the hottest month, indicating noses becoming narrower in hotter, drier areas. No relationship was found between nasal breadth and the humidity variables. The nasal index indicates relatively broader noses in the more humid, tropical zones and relatively narrower noses in the hotter, drier regions. Hiernaux and Froment link this pattern to the air saturation and warming hypothesis of nasal function (Hiernaux & Froment 1976: 766). In their other results, total facial height had only one significant correlation with altitude, and facial breadth both absolute (bizygomatic breadth) and relative (facial index), was found to be wider in wetter, more humid areas, and narrower where it was drier and hotter (Hiernaux & Froment 1976: 766). These results may suggest that it is the moisture content of the air rather than its temperature that produces the selective pressure for nasal narrowness. However, the fact that facial breadth also shares this pattern of distribution indicates that the situation may be more complex.

Europe and the Mediterranean

Crognier has done the only work on ecogeographic variation in craniofacial morphology for Europe and the Mediterranean. His materials and methods were discussed above, and the results of his correlation and stepwise multiple regression analyses are presented in Tables 3.19 through 3.21.

Table 3.19: Summary of correlations between facial and climate variables in European, Middle Eastern and North African males, adapted from Crognier, 1981b: 102.

Variables	n	Mean Ann Temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
Morph face height	81	-0.48**	-0.51**	-0.41**	0.35**	0.22*	0.07	0.22*	0.19
Bizygomatic breadth	81	-0.68**	-0.62**	-0.64**	0.36**	0.44**	0.33**	0.47**	0.24*
Facial index	81	0.16	0.08	0.18	-0.02	-0.18	-0.20	-0.22*	-0.03
Nose height	82	-0.54**	-0.54**	-0.54**	0.35**	0.32**	0.19	0.34**	0.25*
Nose breadth	82	0.05	0.03	0.12	0.11	-0.21	-0.29**	-0.05	0.13
Nasal index	82	0.59**	0.54**	0.60**	-0.27*	-0.47**	-0.39**	-0.37**	-0.16

(* p ≤ 0.05; ** p ≤ 0.01)

Table 3.20: Summary of correlations between facial and climate variables in European, Middle Eastern and North African females, adapted from Crognier, 1981a: 613.

Variables	n	Mean ann temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
Morph face height	32	0.05	0.06	0.22	0.12	0.02	-0.01	-0.02	-0.10
Bizygomatic breadth	33	-0.43*	-0.50**	-0.26	0.21	0.32	0.34	0.30	0.07
Facial index	32	0.26	0.55**	0.39*	0.06	-0.19	-0.27	0.44	-0.11
Nose height	31	-0.10	-0.30	0.06	0.19	0.04	0.11	-0.24	-0.23
Nose breadth	33	0.12	0.16	0.43*	0.10	-0.31	-0.16	-0.46**	0.02
Nasal index	31	0.30	0.21	0.18	-0.10	-0.23	0.12	-0.11	0.29

(* p ≤ 0.05; ** p ≤ 0.01)

Table 3.21: Results of a multiple stepwise regression analysis between facial and climate variables in European, Middle Eastern and North African males, adapted from Crognier, 1981b: 104.

Variables	n	Mean Ann Temp	Mean temp cold month	Mean temp hot month	Mean ann temp range	Mean ann rainfall	Mean rain wet month	Mean rain dry month	Mean altitude
% contribution to the analysis									
Morph face height	81	-	25.68	-	-	-	-	-	-
Bizygomatic breadth	81	46.31	-	-	-	-	3.39	-	-
Facial index	81	-	-	-	-	-	1.13	5.00	-
Nose height	82	2.18	29.42	4.95	3.27	-	-	-	-
Nose breadth	82	-	-	-	-	-	8.13	-	8.96
Nasal index	82	-	-	35.72	3.93	4.62	-	-	1.47

Crognier's results show that in the male sample, nasal height decreases where the climate is hot, but increases where it is wet, and that nasal breadth increases where it is wet, but is unrelated to temperature. As a result nasal index is high (relatively broad) where temperatures are hot and dry, and low (relatively narrow) where the climate is cold and wet and where there is large annual variation in temperature (Crognier 1981b: 103).

Interestingly nose height is directly related to altitude, a result also found by Hiernaux in Africa. The female sample shows a somewhat different pattern, with broader noses in hot, dry regions, but with nose height and nasal index both failing to attain significant correlations (Crognier 1981a: 613). The results of the stepwise regression analysis on the male sample shows that the variable most affected by climate is nose height. Climate is found to predict only about 17% of variation in nose breadth, but almost 40% of nose height (Crognier 1981b: 104). Apart from the correlations with temperature range and altitude, these findings are opposite to those of Hiernaux's study in Africa. This highlights the difficulty in comparing studies where samples are drawn from regions with very different distributions of climate and habitat.

As for other facial variables: in males both morphological facial height and bizygomatic breadth increase where the climate is colder and wetter. The face increases in overall size rather than shape and thus there is no correlation between climate and facial index. The pattern for females is again somewhat different with only bizygomatic breadth attaining significant correlations. Facial shape, as measured by the facial index, produces significant positive correlations with temperature indicating a relatively narrow female face in hotter regions. The stepwise regression on the male sample indicates that bizygomatic breadth is the variable most affected by climate, with about 46% of the variation explained by mean annual temperature. The next most affected is morphological facial height with almost 26% of its variation explained by mean temperature of the coldest month (Crognier 1981b: 104).

The overall results of the stepwise regression analysis supports the earlier studies of Thomson and Buxton (1923) and Davies (1932) that give temperature precedence over moisture as the most influential factor in the ecogeographic patterning of craniofacial morphology. However, as Crognier uses rainfall as his only moisture variable it is difficult to compare his results the studies that use relative or absolute humidity.

Australia

Australia has been the subject of at least three of studies assessing the effect of climate on cranio-facial morphology. Two of these (Wolpoff 1968, and van Holst Pellekaan 1990) involved collections of Aboriginal crania from the east coast of New South Wales. The other (Macho & Freedman 1987), utilised Andrew Abbie's database of living populations from the central section of Australia.

In his 1968 paper Wolpoff used the measurements collected by Freedman (1964) on 55 Aboriginal crania which Wolpoff then sub-divided into three regional samples. He hypothesised that noses should become relatively narrow, as the climate became colder and drier. Wolpoff found this hypothesis confirmed as the breadth of the nose in his sample groups decreased from north to south: that is, they were narrower where the temperature was lower and the air drier (Wolpoff 1968: 413). There was not, however,

any apparent relationship between climate and nasal height (Wolpoff 1968: 413-414). The decrease in nose breadth was in stark contrast to some of the other facial dimensions that increased north to south. Thus populations in the south had somewhat longer and significantly broader faces, with absolutely and relatively narrower noses (Wolpoff 1968: 412-413). Wolpoff concluded that this "real" narrowing of the nasal aperture was a climatic adaptation (Wolpoff 1968: 413). His results, however, are based on a very small sample with little in the way of temporal control.

Measuring crania sourced from a similar area to those used by Wolpoff (indeed their samples probably overlap), but using a vastly different methodology, Sheila van Holst Pellekaan (van Holst Pellekaan 1990) came to very different conclusions to Wolpoff. van Holst Pellekaan was particularly interested in testing the hypotheses of increasing brachycephalisation and decreasing nasal breadth with a decrease in temperature. The former will be discussed in the next section. Her sample included 73 adult male and 60 adult female crania, and 60 male and 41 female mandibles of Holocene Aboriginal populations from the East Coast of Australia (Cape York to Eden) (van Holst Pellekaan 1990: 19-20). van Holst Pellekaan took 25 standard cranial measurements and collected data on one geographic variable (latitude) and three climatic variables (average annual temperature, mean minimum temperature of the coldest month and average annual rainfall). She used combinations of bivariate (standard Pearson's *r*) and multivariate (raw and rotated principal components and cluster analysis) methods to elucidate the relationships between the cranio-facial and climate variables, and between the sample groups themselves. The results of her bivariate correlations are presented in Table 3.22. Unfortunately the author only presented significant correlations in her thesis.

Table 3.22: Summary of correlations between facial and mandibular variables, and location and climate variables, adapted from van Holst Pellekaan (1990): 37

Variables	Latitude	Average Annual Temperature	Minimum Temperature July (Winter)	Average Annual Rainfall
Nasion-Prosthion	-	-	-	-0.36**
Nasion-Nasospinale	-	-	-	-0.40**
Nasal Protrusion	0.24*	-	-	-
Bi-Ectomalare	-	-	-	-0.29*
Mandibular Length	0.36**	-0.39**	-0.32*	-
Bigonial Breadth	0.42**	-0.45**	-0.50**	-0.36*

(Only significant correlations were reported * $p \leq 0.05$; ** $p \leq 0.01$.)

The author found no correlation between climate and nose breadth, however nasal height and prominence were greater where average annual rainfall was lower and in the south. Correlations with rainfall indicate that faces were also longer and palates broader to the south and shorter and narrower to the north. Mandibles became larger as latitude increased and temperature decreased. The female crania and mandibles showed a similar

pattern in the direction of the correlations but were dissimilar in the level of significance when compared with the male sample (van Holst Pellekaan 1990: 37-39).

The correlations between the unrotated principal components of the cranium and mandible and the climate variables are presented in Table 3.23. Again, only significant correlations were reported by the author. As a result PC1 (Cranium and Face), a component of cranial size is missing as it was found to be uncorrelated with any of the location or climate variables.

Table 3.23: Summary of correlations between unrotated principal components of the male head, face and mandible with location and climate variables adapted from van Holst Pellekaan, 1990.

Principal Components	Latitude	Average Annual Temperature	Minimum Temperature July (Winter)	Average Annual Rainfall
Cranium and Face				
PC2	-	-	-	-0.23
PC3	-0.25	0.27	0.25	0.25
Mandible				
PC1	0.42	-	-0.39	-0.45
PC2	0.29	-0.29	-0.30	-
PC3	0.36	-0.36	-0.28	-

(PC2 cranium and face represents facial forwardness, palate size and nose breadth vs cranial size; PC3 represents frontal height and curvature vs mid-facial breadth and nose protrusion. PC1 mandible represents size; PC2 represent length vs breadth and PC3 represents posterior breadth.)

Whilst van Holst Pellekaan concluded that there was evidence suggesting a link between some facial variables (for instance nasal protrusion) and climate, other elements of nose shape were found not to be as clearly related. The author argued that this was the result of the strong inter-correlation of naso-facial variables. Her major finding was that larger mandibles and palates, combined with a relatively broad and more prognathic face was typical of southern populations (van Holst Pellekaan 1990: 122). In females the findings of a more protrusive nose and longer palate were repeated (van Holst Pellekaan 1990: 123).

The results of this study regarding the relationship between nose shape and climate are, therefore, equivocal. They contrast with those of Wolpoff (1968) in not finding a diminution in nose breadth north to south, however the increase in nasal protrusion over the same area fulfils both Wolpoff's predictions, and the conclusions of Carey and Steegmann (1981) regarding the importance of nose depth to adaptation in nasal shape. van Holst Pellekaan notes that some of the variables showing correlations with climate (particularly those of the mandible) have never before been suspected, or claimed, to be subject to climatic selection. This suggested to her that the clines in size and shape that her analysis revealed were due not to climatic selection, but perhaps to mastication forces (and thus diet) and "may reflect correspondence with different resources from the land which in turn is a reflection of climatic conditions" (van Holst Pellekaan 1990: 132).

The final study to be reviewed here is that of Macho and Freedman (1987) that uses Abbie's collection of anthropometric measurements taken on living Aboriginal males and females (see Section 3.3.4.3.2, above). The results of their stepwise regression analysis are presented in Tables 3.24 and 3.25.

Table 3.24: Results of a multiple stepwise regression analysis between facial and climate variables in Australian Aboriginal males, adapted from Macho and Freedman, 1987: 44, Table 10.

% Contributions to the regression analysis							
Variables	Rain Jan	Max Temp Jan	Min Temp July	Temp Range Cold Month	Hum Jan	Hum July	Multiple <i>r</i>
Nose/Mouth							
Nasal H	-	-	-	17.99**	-	-	0.42**
Nasal B	-	-	-	-	2.03**	-	0.14*
Nasal Tip B	-	-	-	4.04**	1.89**	22.65**	0.53**
Nasal D	7.86**	15.68**	-	7.34**	4.98**	-	0.60**
NI B/H	-	-	-	-	-	10.28**	0.32**
NI D/B	1.54**	3.65**	-	7.64**	17.67**	-	0.55**
Face							
Bizygomatic	-	-	-	7.67**	-	-	0.28**
Bigonial	-	-	-	-	6.14**	-	0.25**
Min Frontal B	2.73**	5.23**	3.00**	-	-	8.43**	0.44**
Interorbital B	-	-	-	48.69**	-	-	0.70**
Total Facial H	-	-	-	-	3.81**	-	0.20**
Upp Facial H	-	-	-	-	3.82**	-	0.20**

(* $p \leq 0.05$; ** $p \leq 0.01$)

Table 3.25: Results of a multiple stepwise regression analysis between facial and climate variables in Australian Aboriginal females, adapted from Macho and Freedman, 1987: 45, Table 11.

% Contributions to the regression analysis							
Variables	Rain Jan	Max Temp Jan	Min Temp July	Temp Range Cold Month	Hum Jan	Hum July	Multiple <i>r</i>
Nose/Mouth							
Nasal H	-	-	-	34.63**	-	-	0.59**
Nasal B	-	-	7.60**	-	-	-	0.28**
Nasal Tip B	7.98**	-	16.61**	-	15.33**	4.38**	0.67**
Nasal D	2.10**	13.40**	-	9.16**	3.62**	-	0.53**
NI B/H	-	-	-	-	-	22.37**	0.47**
NI D/B	-	-	-	-	-	29.74**	0.55**
Face							
Bizygomatic	-	-	-	-	-	-	-
Bigonial	-	-	-	8.42**	9.04**	10.15**	0.53**
Min Frontal B	-	-	-	-	-	-	-
Interorbital B	-	-	-	34.10**	-	-	0.58**
Total Facial H	-	-	-	8.88**	-	-	0.30**
Upp Facial H	-	-	-	-	-	16.48**	0.41**

(* $p \leq 0.05$; ** $p \leq 0.01$)

Their results indicate that all nasal variables share some variance with at least one climate variable, although in certain cases it is of a negligible amount. In nasal breadth,

for instance, only about 2% of variance of the male sample is explained by January (summer) humidity, while in the female group only 7.6% is explained by the minimum temperature of the coldest month. This is despite the fact that there are considerable mean differences between groups for nasal breadth (Macho & Freedman 1987: 47). Nasal height, on the other hand, appears to be much more sensitive to climate, sharing almost 18% and 34.6% of its variance, in male and female groups respectively, with temperature range in July (winter) (Macho & Freedman 1987: 46-47). Nasal depth exhibits a more complex pattern of associations, spreading its variance between a number of climate variables, the most important of which is maximum January temperature (Macho & Freedman 1987: 46). Both nasal indices are associated with humidity variables, particularly in the females (Macho & Freedman 1987: 47). However, the factor most affected by climate was nasal tip breadth, though whether climatic selection can be implicated in its variation is highly debatable. Humidity was the major influence for this trait and in females minimum temperature was also important (Macho & Freedman 1987: 47).

The situation for the facial variables is more complex, and in many cases they exhibit different patterns of correlations in males and females. In general, the effect seems to be greater in the female sample (Macho & Freedman 1987: 48). The only variable on which the males and females agree is interorbital breadth, which has its highest inter-correlation with temperature range of the coldest month. This variable accounts for 48.7% of the variation in males and 34.1% in females (Macho & Freedman 1987: 46). Summer rainfall and summer and winter temperatures account for relatively little variation in facial morphology whereas temperature range of the coldest month and humidity account for a much larger proportion (Macho & Freedman 1987: 44-45). The authors, however, are cautious about arguing for a direct relationship between climate and cranio-facial variation in Aboriginal crania. Like van Holst Pellekaan, they suggest an indirect link via diet arguing that:

"Variation in the demands placed on the masticatory apparatus would have selective influence on teeth, muscle size and hence bony attachments. Furthermore, the transmission of stresses from the muscle attachments and the occluding teeth would also affect bony features and particularly breadth dimensions. ... The nature of the unrefined Australian Aboriginal diet would foster the evolution of large teeth, masticatory muscles and the associated bony structures. Further the use of the incisors and canines as tools in the Australian Aborigines, e.g. for stripping bark, sharpening spears, etc. (Barrett 1977) could add to the forces which pass through the interorbital region and could thus influence its dimensions" (Macho & Freedman 1987: 51).