THE ARCHAEOLOGY OF MISSION SANTA CATALINA DE GUALE: 2. BIOCULTURAL INTERPRETATIONS OF A POPULATION IN TRANSITION

CLARK SPENCER LARSEN
EDITOR AND CONTRIBUTOR

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INTRODUCTION

DAVID HURST THOMAS

This is the second monograph in the series entitled The Archaeology of Mission Santa Catalina de Guale. In 1972, the AMNH entered into an agreement with the Edward John Noble Foundation to encourage and facilitate scientific research on St. Catherines, a barrier island off the coast of Georgia. The resulting program has enabled hundreds of scientists and advanced students to carry out research on various aspects of the natural and cultural history of the island. Each year since 1974, field crews from the AMNH have conducted intensive and extensive archaeological investigations as part of this research. The results of these inquiries have been reported in several monographs grouped under the general rubric The Anthropology of St. Catherines Island; each appeared as an Anthropological Paper of the American Museum of Natural History. The first volume in this series (Thomas et al., 1978) provides an overview of the natural and cultural history of St. Catherines Island, and should be viewed as a backdrop for this monograph as well.

THE BIOCULTURAL ANTHROPOLOGY OF ST. CATHERINES ISLAND

The early objectives of the St. Catherines Island Anthropological Project were decidedly biocultural in emphasis, initially focusing on the Refuge and Deptford mortuary complex (Thomas and Larsen, 1979). As a direct outgrowth of these excavations, Larsen (1982) examined a skeletal sample of more than 600 individuals, finding that the shift to agriculture-based subsistence coincided with a general rise in infectious disease, a modification he attributed primarily to increasing population density and a diet high in carbohydrates. The program in mortuary archaeology continued in 1977 and 1978, when two St. Catherines period burial sites were excavated and analyzed (Larsen and Thomas, 1982). More recently, we have reported the results of archaeological excavations of two additional prehistoric burial mounds on St. Catherines Island (Larsen and Thomas, 1986). Other related mortuary excavations are reported elsewhere (Thomas et al., 1977).

EXCAVATIONS AT MISSION SANTA CATALINA DE GAULE

For the last decade, our primary research objective on St. Catherines Island has been the search for and excavation of 16th/17th century Franciscan mission, Santa Catalina de Guale. In the first monograph in this series (Thomas, 1987), we described our motivation for seeking Santa Catalina, and explained how we did it (see also Thomas, 1988).

Throughout most of the 17th century, St. Catherines Island represented the northernmost extension of effective Spanish control in eastern North America. When Santa Catalina was overrun by British forces in 1680, the Spaniards and the Guale began their inexorable retreat southward. The fall of Santa Catalina marked the beginning of the end for Spanish control of the Eastern Seaboard.

The Guale Indians were among the first indigenous peoples encountered by Europeans exploring north of Mexico. They are the best known of the 16th and 17th century Muskogean peoples. Nevertheless, even basic issues of their subsistence and social organization remain today the subject of controversy. A primary objective underlying the search for Santa Catalina was to shed light on the cultural ecology of these peoples. Specifically, in our Santa Catalina excavations, we attempted to address questions of ecological potential, economic change (particularly the relative importance of horticulture), degree of transhumance, relationship of health to social status, and changes in population size among the protohistoric Guale.

Our research at Mission Santa Catalina also had a methodological aspect. Several remote sensing techniques were employed to locate the mission complex, to define the configuration of subsurface structures prior to excavation, and to build a baseline library of geophysical signatures to be projected against in-the-ground archaeological evidence.
Preliminary proton magnetometer research disclosed the presence of a Spanish period barrel well and the ruins of two wattle-and-daub buildings—the church (iglesia) and the presumed kitchen (cocina). Low-altitude aerial photography defined a shell-covered forecourt (atrio) fronting the mission church.

Soil resistivity studies turned up a third wattle-and-daub mission building—apparently the Franciscan friary (convento)—plus a series of contemporary aboriginal Guale structures (in the pueblo). Subsequent ground-penetrating radar survey and low-level aerial photography suggested the presence of a western bastion and palisade trenches surrounding the central mission complex.

RELIGIOUS ARCHITECTURE

After a decade of excavating, we now recognize two distinct churches at Mission Santa Catalina. We know from historical records that the 16th century iglesia was burnt to the ground in September 1597; these ruins were personally inspected by Governor Canzo, who had traveled north from St. Augustine to observe for himself the aftermath of the Guale Rebellion (discussed in Geiger, 1937: 103–104). After a period of abandonment, Santa Catalina was resettled by the Spanish in 1604, and the mission church was reconstructed (apparently on the 16th century site). Although we are still working out the detailed stratigraphic relationships, “Structure 1” at Santa Catalina is, without question, the 17th century church, abandoned shortly after the British siege in 1680. An earlier, somewhat larger, structure also stood in this site, perhaps the remains of the 16th century church, destroyed in 1597.

We know little about the earlier structure, and most of our archaeological evidence relates to the latest church at Santa Catalina, constructed on a single nave plan, lacking both transept and chancel. The church facade, facing southeast, was probably constructed of wattle-and-daub anchored to four round uprights set in shell-lined postholes. Although the facade wall is only about half the length of the lateral walls, these supportive uprights are more than twice the size of corresponding members employed elsewhere in the latest church at Santa Catalina. Apparently a pointed gable was elevated to support a steep thatch roof, or perhaps the facade had a false front projecting above the single-story construction of the nave.

The lateral church walls were constructed both of wattlework and wooden planking. The nave portion was built entirely of wattle-and-daub which, when encountered archaeologically, consisted of a densely packed archaeological scatter.

The symbolic separation between nave and sanctuary was emphasized by a composite construction technique. The sanctuary (northwestern) end of the church, constructed entirely of wooden planking, was apparently elevated above the lateral wattle-and-daub walls of the nave. A clearly demarcated sacristy was built on the Gospel side of the church (the left-hand side of the sanctuary as one faces the altar). This room was presumably used for storage of vestments, linens, candles, processional materials, and other ritual paraphernalia essential to performance of the Mass. Inside the sacristy we found a cache of charred kernels, and all grains so far examined have been provisionally identified as wheat, Triticum spp., a significant find in Spanish Florida (as discussed in Thomas, 1988). We suspect that this wheat was destined to be baked into the “host,” flatbread used in the Eucharist. If so, then this lowly wheat cache underscores the effectiveness of the Franciscan Order in obtaining the supplies necessary for the proper conduct of Church ritual—even on the most remote northern frontier of the Guale province.

Roman Catholic liturgical regulations—and a sense of architectural balance—further dictate that a second room must have been built on the opposite side of the altar, to balance the sacristy. But we presently lack evidence for such a room.

Fronting the church at Santa Catalina is a square shell-covered subplaza, measuring about 15 m on a side. This churchyard (or atrio) was probably a low-walled enclosure demarcating the public entrance to the church. Ubiquitous features of New World religious architecture, churchyards served not only as a decorous entryway into the church, but also variously functioned as outdoor chapels, areas to contain overflow congregations, and sometimes as cemeteries (although no human bur-
ials have been found in this area of Mission Santa Catalina.

The churchyard at Santa Catalina was constructed of water-rolled marine shell, available from naturally occurring deposits scattered along the intracoastal waterway; these massive shell bars, accessible only by watercraft, today continue to provide building aggregate. Low-level aerial photography has disclosed a faint pathway leading across the atrio into the church doorway. This narrow line of crushed, compacted shell was created by hundreds of 17th century processions, neophytes moving single-file to attend services at Santa Catalina.

The only known cemetery at Santa Catalina occurs inside the church, and this mortuary population provides the empirical evidence considered by Larsen and his collaborators in this monograph. By employing a series of generalized stress indicators and specific nitrogen- and carbon-isotope technology, they attempt to monitor dietary changes (especially the dietary importance of maize) and determine the nature of demographic and behavioral shifts among Native Americans in Spanish Florida. The analyses to follow likewise provide information regarding pathology, bone size modification, and the relationship of social status to resource access.
CHAPTER 1. BIOLOGICAL INTERPRETATION AND THE CONTEXT FOR CONTACT
CLARK SPENCER LARSEN

ABSTRACT

During the contact period, native populations were subject to a variety of stressors, including but not limited to, epidemics, food shortages, labor demands, retaliation by the Spanish following revolts, and attacks originating in the English-occupied Carolina colony. Increased sedentism and centralization of population, coupled with a greater reliance on plant domesticates, especially maize, and an overuse and depletion of already poor soils, undoubtedly resulted in related disease and nutritional problems as well as alterations in mechanical behavior.

INTRODUCTION

The arrival of Europeans in the New World and the consequences of contact for aboriginal populations have been areas of intense interest to a wide range of scholars, including historians, demographers, and anthropologists. Working primarily with the aid of written documents—such as census records, accounts by explorers, mission priests, and others—investigators have provided details of these consequences, particularly with regard to the remarkable decline in population size for a number of geographic regions in the Americas (cf. Brasser, 1978; Trigger, 1985; Kelley, 1988; Kelley and Robinson, 1989; Fausz, 1985; Turner, 1985; Wood, 1987; N. Cook, 1981; Hemming, 1978; Robinson, 1981; Borah, 1964; S. Cook, 1937, 1966, 1973a, 1973b, 1976; S. Cook and Borah, 1971, 1974; Castillo, 1978; Jackson, 1983, 1986; Langer and Jackson, 1988; Stern and Jackson, 1988; Simmons, 1979; Kelsey, 1984; Reff, 1985; Schuetz, 1980; Denevan, 1976; Danubio, 1987; Sauer, 1966; Ramenofsky, 1987; Dobyns, 1983; Milner, 1980; M. Smith, 1987; Fish and Fish, 1979; Wood et al., 1989; Lehmer, 1971; Bradtmiller, 1983; Dumond, 1986; Fagan, 1984; Jennings, 1975; Crosby, 1972, 1986; Thornton, 1987; Ubelaker, 1988; and others).

Until recently, the impact of European contact as it is revealed archaeologically has received limited attention (see discussions by N. Cook, 1981; Ramenofsky, 1987; M. Smith, 1987). In the bioarchaeological record in particular, very little attention has been given to human skeletal remains as a data source in the interpretation and understanding of post-contact biocultural adaptation in the New World. Exceptions to this include ongoing research by Owsley and co-workers (Owsley, 1980; Owsley et al., 1977; Owsley and Bass, 1979; Owsley and Bradtmiller, 1983; Owsley and Jantz, 1983; Bradtmiller, 1983, 1985) and Palkovich (1981) on the Arikara; Cohen and co-workers (Cohen, 1987; Danforth, 1988; Danforth et al., 1985) on the Maya; Kelley and co-workers (Kelley, 1985, 1988; Kelley, Barrett, and Saunders, 1987; Kelley, Ledzik, and Murphy, 1987; Robinson et al., 1985; Clark et al., 1987) on the Narragansett; Blakely and co-workers on the Coosa (Blakey and Detweiler, 1985; Blakely, 1988; Blakey and Detweiler-Blakey, 1989); Buikstra (1976) on the Caribou Eskimo; Meer and co-workers on native Alaskans (Meer, 1985; D. Cook, 1985); Walker and co-workers (Walker, n.d.; Walker et al., 1989; Costello and Walker, 1987) on native Californians; and Miller (1989; see also Humphreys, 1969) on missions of Texas.
In order to fully understand the nature of biological adaptation of contact-period native populations in a given region, it is important that a large, well-documented series of human remains be available for that region representing the period of time prior to the arrival of Europeans. By documenting the record of biological adaptation prior to European contact, a context is established for interpretation of biological change in the contact period relative to the period of time predating the arrival of non-native populations. The Georgia coast represents an ideal locality for such interpretation in that a large sample of human remains from precontact sites has been recovered and studied, thus providing the basis for comparison with contact-period human remains.

It is the purpose of this monograph to present findings from a bioanthropological research program that address directly the issue of European contact and its role in native biological adaptation and lifeway in general. By study of a series of human remains recovered from Santa Catalina de Guale on St. Catherines Island, Georgia, and comparisons made with precontact St. Catherines Island (e.g., Larsen and Thomas, 1978, 1982, 1986; Thomas and Larsen, 1979) and other Georgia coastal populations (reviewed in Larsen, 1982), it is hoped that the importance of human remains in addressing these and related issues will be demonstrated.

The study of the human remains from Santa Catalina provides an important perspective on the human populations during the contact period in Spanish Florida. Although a great wealth of archaeological data has surfaced during the last decade from this site and others in La Florida (see Thomas, 1987), it is only through the study of the human remains that we see direct evidence for the dramatic alterations in lifeway and adaptation after the arrival of Europeans.

The first volume of the present monograph series (Thomas, 1987) introduced important background and should be consulted prior to reading this volume. In this chapter, I highlight pertinent information drawn from that volume and elsewhere in order to provide biocultural, ethnohistorical, and archaeological contexts for the ensuing chapters. It is anticipated that some of the gaps in our knowledge of biocultural change outlined below will be filled in by the contributions presented in this volume.

**THE BIOCULTURAL CONTEXT**

Human populations occupied the Georgia coastal region for some 4000 years prior to European colonization (Thomas et al., 1978; Larsen, 1982). The area was undoubtedly quite attractive to native inhabitants because of its great estuarine and marine productivity (Reitz, 1988). The estuaries of the southeastern Atlantic coast are some of the most productive in the world and are the most productive along the Eastern Seaboard (Reitz, 1988). Archaeological evidence for the period of time prior to European contact indicates that hunting, gathering, and fishing provided the basis for the subsistence economy. Analysis of food remains from a large number of sites shows that marine resources—both vertebrates (e.g., fishes) and invertebrates (e.g., shrimp, oysters, crab, clams, whelks)—provided the majority of protein (Reitz, 1982a, 1982b, 1985, 1988; Reitz and Scarry, 1985; Reitz and Quitmyer, 1988; Quitmyer et al., 1985).

Terrestrial resources were of secondary importance. Among these were several types of nuts, including mostly hickory nuts and acorns that were collected during the mature phase (Larson, 1980; Reitz and Scarry, 1985). Other plant resources include chinquapins, black walnuts, beach nuts, blueberries, palmetto berries, persimmons, and a variety of edible roots and tubers (cf. Reitz and Scarry, 1985). Animals available as food included mostly deer, but opossums, raccoons, rabbits, squirrels, bears, bobcats, foxes, and other mammals, several reptiles and amphibians, and a variety of birds were also consumed (Larsen, 1982; Reitz and Scarry, 1985; Reitz, 1988).

The role of plant domesticates in Georgia coastal native diets has been a subject of debate (see reviews in G. Jones, 1978; Larsen, 1982; Thomas, 1987). Archaeological evidence suggests that maize, in particular, may have become important in the subsistence regime during the 12th century A.D. The botanical evidence is rather meager on this point.
(cf. Larsen, 1982; Thomas, 1987; Reitz, 1988), but the appearance on the Georgia coast of large, nucleated settlements as well as a probable increase in population and more sedentary lifeway are consistent with a population model associated with the Mississippian period in eastern North America (cf. Steponaitis, 1986; B. Smith, 1986). That is, in addition to hunting, gathering, and fishing, maize agriculture was practiced as an important part of the subsistence economy during the last few centuries prior to the arrival of Europeans in the New World.

The effects of increase in sedentism and population size, density of population, and intensification of food production are becoming well-known points of discussion in archaeological studies. With regard to coastal and island populations, the arrival of agriculture has recently been examined in some detail in such diverse contexts as Denmark (e.g., Rowley-Conwy, 1984) and Japan (e.g., Akazawa, 1982). Evidence from these areas suggests that the shift to agriculture may have arisen as a result of resource stress, particularly as it is represented by a decline in availability of shellfish. Reasons for the adoption of agriculture on the Georgia coast remain elusive, however, because shellfish and marine resources in general appear to have been important throughout the entire archaeological record, both before and during contact by Europeans (cf. Reitz, 1985; Reitz and Scarry, 1985). Waselkov (1987) has suggested that if plant domesticates did not fully meet protein requirements in human societies, then shellfish collection would continue. In most areas of the world where agriculture becomes a dominant resource, shellfish gathering shows an apparent decline. It is not clear as to whether or not shellfish gathering declined on the Georgia coast during later prehistory.

An important index of resource stress in island and coastal environments has been provided by the study of morphological and age-structure changes in the remains of shellfish recovered from archaeological sites. A number of workers have documented a reduction in size or survivorship or both in shellfish populations from a number of different contexts (e.g., Swadling, 1977; Spennemann, 1987), suggesting an increase in predation of these resources. Study of resource stress based on analysis of the hard clam (Mercenaria mercenaria) by Quitmyer and co-workers (1985) has provided some information with respect to the Georgia coast. These investigators have shown that mean age-at-death of clams from late Archaic, Woodland, and Mississippian period contexts declined. In particular, Mississippian period clams were significantly younger than the clams from the earlier periods. It was concluded that these age profile changes reflect an intensification of human exploitation of local clam beds due either to heavier reliance on hard clams or an increase in human population in the region. Although resource stress may have been specific to shellfish in Georgia coastal and other populations, it can be argued that the declines in this resource may, in fact, reflect declines in availability of other resources. However, although subsistence change quite likely has occurred here, it is important to point out that, taken alone, change in food sources does not necessarily indicate pressure arising from population increase (cf. Cohen, 1977; Hassan, 1981; Sullivan, 1987).

The human biological consequences of resource stress in general and the adoption of agriculture in particular have been studied from a range of contexts worldwide (various studies in Cohen and Armelagos, 1984), including the Georgia coast (Larsen, 1981a, 1981b, 1982, 1983a, 1983b, 1983c, 1984; Larsen and Ruff, in press; Ruff et al., 1984). The adoption of agriculture and its impact on human health and overall well-being shows a number of common themes globally. That is, the adoption of agriculture saw a general decline in health and quality of life (Cohen and Armelagos, 1984; Roosevelt, 1984), along with a number of skeletal and morphological alterations reflecting behavioral modifications associated with changing work patterns and physical demand.

With regard to coastal Georgia, the behavioral shift from hunting, gathering, and fishing to a lifeway that focused at least in part on maize agriculture included a number of morphological and health-related factors: (1) increase in nonspecific bone infection; (2) increase in dental caries; (3) decrease in degenerative joint disease (osteoarthritis); (4) decrease in craniofacial, tooth, and postcranial
size; (5) decrease in skeletal robusticity and bone strength; and (6) decrease in body size and stature. Although each of these findings was made on specific biological characteristics, it is more appropriate to view them in the context of an interactive process (fig. 1-1) involving changes in settlement pattern (nucleation and sedentism), work load (on the body and masticatory apparatus), and food composition and nutritional adequacy (carbohydrate consumption, protein quality). Viewed from this processual perspective, these skeletal changes are certainly consistent with a lifeway associated with the adoption of agriculture shown in other areas of the world (cf. Cohen and Armelagos, 1984).

Although the particulars of these changes are not entirely understood, it can be concluded that for the prehistoric Native Americans inhabiting the Georgia coast in general, and St. Catherines Island in particular, the shift occasioned a decline in quality of life and a decrease in mechanical loads associated with the addition of agriculture to the dietary regimen. The decline in quality of life is not on the same order as that documented for other Mississippian populations (e.g., Dickson Mounds [Goodman et al., 1984], and Averbuch [Eisenberg, 1986]). Nevertheless, it is clear that things took a turn for the worse in many respects.

The general decline in quality of life on the Georgia coast appears to have had a differential impact with regard to gender. That is, study of specific indicators of health, including body size and stature, nonspecific infection, and dental decay, reveals a relatively greater impact on females than males in the transition to agriculture. For example, although both sexes in the agricultural period experienced reduction in body size and stature, the reduction in adult females was rel-
Relatively greater than in adult males. These findings are contrary to the consensus that males are more vulnerable to environmental stress than are females (cf. Stini, 1969). Stinson (1985) has argued, however, that there is only weak support for the hypothesis that males are less buffered against environment than females (see also Larsen, 1987; Clark, 1988). Indeed, the greater frequency of dental carious lesions and bone infections in females than males in the agricultural period on the Georgia coast (Larsen, 1982, and references cited above) would suggest quite the opposite, at least with regard to this setting. Clark (1988) has examined indicators of growth disruption in the Dickson Mounds series. This investigation, too, demonstrated quite clearly that females experienced greater environmental stress in the transition to agriculture than males.

With the arrival of the Spanish in the 16th century, how did native diet, subsistence economy, and lifeway in general change? The available data indicate that although Old World plants (e.g., wheat) and animals (e.g., cattle, pigs, chickens) were introduced to the Florida provinces by the Spanish, they appear to have had very limited importance for the Guale (Reitz and Scarry, 1985). Unfortunately, most of the archaeological record of food remains is not from mission or native contexts. Nevertheless, evidence suggests that marine resources continued to play a role in Guale foodways, but it is not known how much.

Larson (1978) suggested that there was a quantitative decrease in the amount of shell deposited in habitation sites by native populations in the contact period. According to Larson, this change in site composition reflects a shift to a sedentary, agricultural economy that placed more emphasis on domesticated plants than wild plants or animals. Waselkov (1987) argued that when human populations begin to focus on agriculture, there is a concomitant reduction in use of shellfish. It is possible that in contact-period archaeological sites on the Georgia coast shell reduction may reflect an increase in emphasis on domesticated plants, but at present, this is not well documented. Clearly, more work needs to be done in this region. Whatever dietary changes did occur, however, it seems likely that the residential shifts during the 16th and 17th centuries were accompanied by subsistence shifts as well (Reitz, 1988).

The limited data from archaeological native contexts are conflicting. Duncan (1987) has recently reported on a sample of faunal remains recovered from a food-processing area at Santa Catalina. Interestingly, wild mammal, especially deer and raccoon, is the largest contributor to the faunal assemblage. Marine resources are only poorly represented. Although it is possible that native populations relied to a much larger extent on wild animal terrestrial populations, this hypothesis seems unlikely given the discussion of maize in Guale diets by missionaries and other Spanish personnel (see below). More likely, these faunal materials reflect the diet of the Spanish at Santa Catalina and not that of the native populations (Reitz, 1988). On the other hand, Reitz (1985) has reported on the faunal materials recovered from middens associated with the Mission Nombre de Dios near St. Augustine. These data suggest that marine resources were the greatest faunal contributor to native diets at that locality. Although the body of evidence at hand is limited, this dietary reconstruction is more similar to native diets for the precontact populations from the region and, therefore, may be more representative of foodways practiced by the Guale than the faunal materials recovered from Santa Catalina.

The botanical evidence is even more meager than the faunal evidence for the contact-period mission populations (see Thomas, 1987). However, the written record for use of maize strongly suggests that it continued to be important into and through the contact period (G. Jones, 1978; contra Crook, 1984, 1986).

THE ETHNOHISTORICAL CONTEXT

The written documentation for the contact period from Guale is spotty in some areas. Nevertheless, it provides a rich record of data not available through archaeological research in the region. From the ethnohistorical documentation by a number of scholars, it is known that the colonization and establishment of missions in La Florida by the Spanish in the 16th century saw radical changes
for native inhabitants. These native inhabitants—the Guale—were among the first of the native populations contacted by European explorers in the Americas north of Mexico (G. Jones, 1978). In the following discussion, I will comment on some effects of these changes.

By all accounts, the most important economic product in Spanish Florida appears to have been the labor provided by natives (Hann, 1988). Given the lack of interest by Europeans in agricultural work, Indians associated with the missions provided the labor force that was necessary for the raising of crops and other subsistence-related activities. This labor force was important not only on the local level, but it supplied workers for projects away from home missions. Recruitment from nonlocal areas was an important means by which the local government obtained native laborers. With reference to growing of crops, in the 1602-1603 report to the crown by Governor Canzo, he noted that but with all this and the grain from the maize, the labor that they endure in the many cultures that are given is great, and, if it were not for the help of the Indians that I make them give, and they come from the province of Guale, Antonico, and from other caciques, it would not be possible to be able to sow any grain . . . (unpublished translation provided by John H. Hann).

This passage strongly suggests that labor demands on natives were intensive and a necessary requisite to the success of Europeans in the region.

Use of native labor appears to have been especially important for production of food for Spanish colonists, soldiers, and clergy. Natives referred to as indios de cava (cultivation Indians) are listed in a recently translated document by Eugene Lyon (n.d.). One Spaniard observed that a great deal of effort went into the preparation of maize flour (cf. Hann, 1986b). The individual went on to note the process involved in preparing the flour: "The hand is the guide for the rammer which is more than two varas (approximately two yards) in height, and the rammer moves upward and the thin end remains in the mortar" (quoted in Hann, 1986b: 98). Among the Apalachee (southwest of Guale), it appears that the young males were responsible for this activity (Hann, 1986b).

Other demands for native labor to satisfy Spanish needs involved construction projects, fortification projects, wood-cutting, cargo-bearing, and other activities, apparently at great expense to natives. Hann (1986a, personal commun.) has noted, for example, that the males recruited for labor in construction projects at St. Augustine were required to lift heavy logs over some distance to the construction site. Native males saw frequent service as ferrymen for trips between Guale and St. Augustine and between St. Augustine and Charleston (e.g., Andrews and Andrews, 1975). These labor practices undoubtedly represented great changes in work patterns and intensity of labor. This repressive system was undoubtedly a factor that led to the decline of native populations.

In the province of Apalachee, Hann (1988) noted that natives were required to carry heavy burdens over great distances to and from St. Augustine, the capital of La Florida. In the 1670s, Fray Alonso Moral provided the following graphic account of conditions of life for native laborers:

All the natives of those provinces suffer great servitude, injuries, and vexations from the fact that the governors, lieutenants, and soldiers oblige them to carry loads on their shoulders to the Province of Apalachee and to other areas and also to bring loads from those regions to the fort of St. Augustine. And it usually happens that to enhance their own interests they pretend that this work is in Your Majesty's service, without paying them what is just for such intolerable work. And if now and again they give them something for that reason, it is a hoe or an axe or a cheap blanket for some other thing of such slight value to pay for their work, which involves carrying a cargo on their shoulders from the fort to the Province of Apalachee, which is eight leagues distant, and the same to return. . . . And in addition to this, in order to employ them further they detained them in St. Augustine for as long as they wish . . . with very short rations, such as giving them only two pounds of corn a day and giving them for pay, at the most, one real for each day of work, which sum is usually given them in the form of old rubbish of little or no value or utility to them. Add to this the further vexation or injury of being snatched by force from their homes and villages, not only for tasks at the fort but also for work for private
citizens, and this in the rigor of winter (when they come naked) or in the middle of summer, which is when they are most occupied in the labor of their crops on which solely depends not only their sustenance and that of their wives and children but also the victuals necessary for the relief of the garrison. . . . Each year from Apalachee alone more than three hundred are brought to the fort at the time of the planting of the corn, carrying their food and the merchandise of the soldiers on their shoulders for more than eighty leagues with the result that some on arrival die and those who survive do not return to their homes because the governor and the other officials detain them in the fort so they may serve them and this without paying them a wage. . . . This is the reason according to the commonly held opinion that they are being annihilated at such a rate (quotation from Hann, 1988: 140–141).

Another use of local natives as a labor source was military service. For example, in 1673, Governor Francisco de la Guerra y de la Vega wrote that 45 to 50 Guale were conscripted in order to make up for gaps in the infantry (Loucks, 1979). The use of native conscripts certainly implies the movement of native males away from the home localities.

Immediately after the establishment of the missions, the native populations were aggregated into centralized villages that were either associated with the missions themselves—as in the case of St. Catherines Island—or with nearby visitas (Loucks, 1979). This concentration of native populations (known as Reducción) into a limited number of areas was a primary objective in the establishment of the missions (Geiger, 1937), and it was envisioned as serving the Spanish authorities in a number of ways. First, centralization served to provide control over the native populations. Second, it served an acculturative function, in part by helping to facilitate the task of indoctrinating natives into Christianity. Third, it provided for an accessible labor pool for activities discussed above. Finally, in addition to economic interests, the mission populations and associated garrisons served as an important link in a defensive network that was perceived as a protective buffer against encroachment of French and British interests from the north (G. Jones, 1978).

With regard to agricultural concerns, a number of areas of Spanish Florida functioned as crop-producing centers. St. Catherines Island is known to have sent large quantities of maize to St. Augustine (Bushnell, 1987). Loucks (1979) has suggested that because of the demands placed on the native populations by the Spanish, increasing amounts of time were spent in food (crop) production. We can infer, therefore, that the amount of workload changed during the historic period.

The manipulations of native populations by the Spanish saw a number of important consequences for the former. It is clear, for example, that the Guale suffered harassment from the military and demands for food tribute (G. Jones, 1978). A direct response to this harassment and other infringements was a series of revolts by the Guale mission native populations as well as in other parts of the Florida provinces. These uprisings, although temporarily successful, resulted in almost certain retaliation by the Spanish in the form of burning of towns and valuable stored crops that were to have been seen the local populations through the winter months. Existing documentation indicates that many Indians lost their lives in these confrontations (G. Jones, 1978), or were otherwise required to provide yet more labor (Hann, 1988).

Other resultant detrimental effects arising during the mission period are seen in political organization. Milanich (1978) noted, for example, that after the missions were established among the Yustega (western Timucua) in 1633 there are no references to chiefs of regions, but only to chiefs of separate villages. Although this observation may represent a bias in the ethnohistoric sources, Milanich (1978) suggested that lack of mention of regional chiefs reflects a breakdown in tribal-level organization and to either decline in importance or disappearance of tribal-level chiefs. This development may, in fact, represent a direct growth of the attempt by the priests to decentralize tribal authority and to increase the importance of the village chief in the belief that the village chief would play a key role in converting the remaining population.

Additional consequences of the mission effort were necessarily brought about by contact with Europeans. In particular, the disease
baggage that had evolved in the Old World and was carried by the Spanish into the New World is a very important factor for understanding the decline and ultimate extinction of native populations. Prior to the arrival of Europeans, there is evidence for the presence of infectious disease in New World populations (e.g., Newman, 1976; Larsen, 1982; Buikstra, 1981; Powell, 1988, this volume; Baker and Armelagos, 1988). However, relative to what was to come, native peoples lived in a relatively disease-free environment, not suffering from viral and bacterial pathogens such as smallpox, measles, chickenpox, influenza, typhus, diphtheria, cholera, plague, whooping cough, or malaria (Dobyns, 1983).

The introduction of these diseases into the New World was devastating. The impact on native populations in the Southeast, in particular, was observed quite early. When the de Soto expedition arrived in 1540 at Cofitachequi (on South Carolina side of the Savannah River), a chronicler of the expedition reported that

Within a league, and a halfe a league about this towne, were great townes dispeopled, and over-grownne with grasse, which shewed that they had been long without inhabitants. The Indians said, that two years before there was a plague in that countrey, and that they remooed to other townes (Elvas, 1851: 51–57).

At nearby Talomeco, another chronicler of the expedition indicated that they

found no people in Talomeco because the previous pestilence had been more rigorous and devastating in this town than in any other of the whole province, and the few Indians who had escaped had not yet reclaimed their homes; hence our men paused but a short time in these houses before proceeding to the temple (Garcilaso de la Vega, 1951: 315).

At Talomeco, the Spanish military encountered 500 deserted houses; four of the largest of the structures were filled with the remains of the recently deceased (Garcilaso de la Vega, 1951).

Epidemic disease devastated the Spanish Florida provinces. No fewer than eight major epidemics probably passed through peninsular Florida prior to 1562 (Dobyns, 1983; and see discussion in M. Smith, 1987). Later epidemics were equally destructive. During the Sir Francis Drake raid on St. Augustine in 1586, at least one and possibly two major epidemics occurred, killing many in a very short time (Dobyns, 1983). In 1596, and again in 1614 and 1617, epidemics were responsible for a large number of deaths and complete depopulation of villages in a number of instances (Dobyns, 1983; Geiger, 1978). Although possibly exaggerated, friars’ estimates indicate that half of the Indian population of Spanish Florida was terminated during the second decade of the 17th century (Bushnell, 1978). A major episode of disease followed in 1672 (Bushnell, 1978).

With respect to the Guale, a number of major episodes of disease are documented. During the years 1569–1570 and 1582, epidemics swept through the missions and surrounding areas. The years 1649–1650, 1657, and 1659 were apparently some of the most devastating years that the Guale experienced (G. Jones, 1978). In 1657, the governor of Spanish Florida observed that there had been drastic reduction of native population of Guale “because they have been wiped out with the sickness of the plague and small-pox which have overtaken them in the past years” (quoted in Hann, 1986a: 378). The decade of 1649–1659 saw the deaths of thousands of individuals.

The huge population losses due in large part to epidemics in this region as well as others in the New World have been a subject of much discussion by medical historians and others. A consensus has developed that native populations likely had greater genetic susceptibility to Old World pathogens because of their lack of immunological experience in comparison with Europeans. Kelley (1988) has suggested, however, that it is unlikely that native populations lacked inherent genetic resistance (see also Newman, 1976). It is quite probable that Europeans maintained an advantage in that their experience with Old World pathogens resulted in acquired immunities for many. Kelley (1988) pointed out that perhaps of greater importance in explaining the devastation in New World populations is the complete lack of knowledge of simple medical attendance for individuals afflicted with viral and bacterial diseases—specifically, rest, warmth, and fluid
consumption. In colonial New England, for example, Kelley (1988) noted that 17th century Europeans were quite aware of the efficacy of these factors in returning the sick to a healthy state. Native populations in the region were not. It may be that the resident priests in Spanish Florida attempted to impart this knowledge to the local populations. The decimation of population in this region would suggest that such attempts were unsuccessful in this endeavor.

Further exacerbating the situation was the factor of population centralization. The mission system aggregated many into more restricted living areas. The villages surrounding the mission complexes, for example, quite likely provided ideal conditions for the spread of the newly introduced Old World pathogens as well as existing indigenous pathogens.

The loss of life among native populations in Florida undoubtedly meant the reduction of the labor source normally available to the Spanish. One Spaniard wrote in 1655 that the devastation of disease had been so severe that Indians could not be relied upon for labor projects associated with the repair of the fort at St. Augustine:

The necessary wood must be cut and brought from the forests by Indians. This necessitates too much work for them as the distance which it must be carried on their shoulders is long. I now consider this manner of bringing it impossible because of the high mortality rate which has been the result of a series of plagues of smallpox which have afflicted the country for the last ten months. Many died as a result of this and of the trials and hunger which these unfortunate people have suffered, and the province is quite destitute (translation from Hann, 1988: 177).

The sum effect of epidemics, forced labor, military and other forms of harassment, and almost certain social disruption was a remarkable population decline, especially during the 17th century. Other factors such as soil depletion due to agricultural overuse and a generally declining environment may have also been important in this decline. Final abandonment of the primary mission of Guale—Santa Catalina de Guale—on St. Catherine’s Island resulted in relocation of the mission and its population on Sapelo Island to the south (Thomas, 1987). Continued predation by pirates and others on this group and other nearby refugee populations, however, resulted in yet another relocation and establishment of the new mission, Mission Santa Catalina de Guale de Santa Maria, on Amelia Island in 1686 (Bushnell, 1987).

**THE ARCHAEOLOGICAL CONTEXT**

Following a program of survey, test excavation, and remote sensing analysis, the precise location of Santa Catalina de Guale was verified by David Hurst Thomas and associates to have been on the western periphery of St. Catherine’s Island (Thomas, 1987, 1988) (fig. 1-2). Preliminary test excavations at the mission church within the site revealed that in addition to the ritual functions normally associated with the church, this structure served as the cemetery for the native inhabitants of the mission complex.

From 1982 until final excavations in May of 1986, I directed the complete excavation and recovery of human remains from the cemetery (fig. 1-3). With the completion of this work, it is possible to describe and summarize some important characteristics of the cemetery at Santa Catalina de Guale. (A complete description of the human remains and the archaeological context will be presented in a future monograph in the present series.) A minimum of 431 individuals of varying states of preservation have been recovered from the mission cemetery (Russell et al., this volume). The years during which burial of these individuals took place are somewhat unclear. However, it is known that the church was burnt to the ground in the 1597 rebellion (see Thomas, 1988). The mission was subsequently resettled by the Spanish in 1604, and the church was rebuilt on the same site as the former structure several years later. Based on a preliminary analysis of artifact associations in individual burial and disturbed contexts, the use of the cemetery appears to have been limited to the 17th century, from A.D. 1607 to 1680 (Thomas, personal commun.). The period of use corresponds to Period III (A.D. 1607–1684) on the contact-period Guale coast (G. Jones, 1978; Thomas, 1987).

The cemetery is confined to an area measuring approximately 20 × 11 m, which corresponds to the size of the church struc-
The facade of the structure faced southeast and was the only wall constructed of wattlework. The other three walls were constructed of largely wattle-and-daub. The entrance of the church was fronted by a large, rectangular churchyard covered with shell collected from nearby natural marine shell deposits. Churchyards are commonly associated with colonial churches, and served a number of functions including burial of the dead. Partial excavation of and remote sensing data collected from the churchyard at Santa Catalina shows that burial of deceased individuals was unlikely in this area (Thom- as, personal commun.). A thorough excavation of this area is needed, however, to determine whether or not human burials are located in the churchyard. Other areas of the mission complex have yielded no human remains.

Unlike Santa Catalina, most other archaeologically documented cemeteries in La Florida are located outside church walls (B. Jones, 1980; Larsen and Saunders, 1987; Thomas, 1988). However, the mortuary program at Santa Catalina is similar to all other urban (St. Augustine) and mission cemeteries in that the hands of the deceased were clasped or folded on the chest or abdomen; and the skeletal remains were in supine, extended positions. At Santa Catalina, the bodies of the deceased were placed in shallow pits—about a half meter deep—that are aligned parallel to the long axis of the church. The heads were oriented east-southeast, away from the facade. A single skeleton was found in association with a coffin in the altar area; all others were either shroud burials or burials lacking covering.

The high degree of disturbance of human remains in the cemetery reflects its intensive use. That is, only 52.4% (N = 226) of the remains were found to be in primary, undisturbed contexts. The remaining 47.6% (N = 205) were recovered in secondary, disturbed contexts. With one exception, all of the disturbance of individuals appears to have occurred during placement of later burials. The single exception involved the intrusion of a large wooden post into a burial located along the west wall.

Most burials represent interments of single individuals. The lack of mass burial would
Fig. 1-3. Map showing location of human remains at Santa Catalina de Guale mission cemetery.
suggest that many, if not most, of the individual deaths were not associated with major epidemics in the region. However, the lack of mass burial certainly does not preclude the presence of epidemics in the region. Ethnohistoric resources would suggest otherwise (cf. Jones, 1978 and discussion above).

Within the cemetery, there are no clear patterns of distribution by age or sex. There appears to be a greater concentration of juveniles along the north wall of the church, but this was not the only location of younger individuals in the cemetery. In other cemeteries excavated in La Florida, there is some evidence for location of burial in relation to age. For example, at Santa Catalina de Guale de Santa Maria (Amelia Island), most young juveniles (less than 10 years) were placed at one end of the cemetery (Larsen and Saunders, 1987; Saunders, 1988).

The artifact inventory from the cemetery is unusually rich. In addition to beads numbering in the thousands—estimated to be in excess of 100,000—there were medallions, rings, mirrors, copper bells, crucifixes, majolica vessels and plates, rosaries, shroud pins, shroud cloth, as well as a variety of aboriginal grave inclusions (chunky stones, Mississippian-style rattlesnake shell gorget, projectile points) that were recovered in the bioarchaeological excavations. Most of the artifactual materials from the cemetery are associated with the end of the church opposite the entrance, suggesting that it is in this area that the altar may have stood. It is interesting to note that the lowest density of human remains occurs in this area of the cemetery. The placement of these individuals in this area of the cemetery may represent their position in relation to key areas within the ritual nucleus of the church, perhaps reflecting a status hierarchy in Guale society. (A discussion of the implications of the presence of this rich artifact assemblage is provided in Thomas, 1988.) Therefore, although there is an apparent lack of age or sex distinctions in location of burial within the church, there appears to have been some form of social distinction in relation to proximity of burial to the altar area. It may be premature, however, to regard this distinction as a simple “high status”/“low status” dichotomy (cf. Thomas, 1988).

Very early in the excavation of the Santa Catalina cemetery, it became quite clear that the skeletal series would be represented by a large number of human remains. This, coupled with archaeological data on architecture, population settlement, food remains, and ethnohistoric documentation, suggested that a detailed biocultural analysis of the human remains would provide an important focus for a better understanding of postcontact adaptations of New World native populations.

The skeletal sample recovered from Santa Catalina de Guale is important in that it represents the first archaeologically well-documented aboriginal mortuary site in Spanish Florida. The locality, however, is not the first contact-period cemetery to be investigated in the region. Native human remains from a number of other series have been excavated and incompletely reported on from mission and nonmission contexts in peninsular Florida (see review in Thomas, 1987). The localities where human remains have been documented include San Damian de Escambi (143 burials), San Jose de Ocuya (300 burials), San Miguel de Asile (10 burials), San Pedro y San Pablo de Patale (65 burials), San Juan del Puerto (scattered skeletal elements), and Nombre de Dios (100 burials). One possible native skeletal individual was recovered from the church/hospital at Nuestra Senora de la Soledad (Koch, 1980), and a number of isolated remains have been reported on from various other settings (H. Smith, 1956).

More recently, however, Mitchem and Hutchinson (1987; Hutchinson, 1989, 1990) have reported on a large series of primary and secondary burials from Tatham Mound on the western Gulf coast of Florida. Human remains from this site are especially significant because of their very early context in the contact period of Spanish Florida (early to middle 16th century).

With respect to the nonpeninsular region of La Florida—the Georgia coast—several isolated skeletons have been described (F. Cook and Pearson, 1973; Braley et al., 1986). In addition, three large series of human remains have been recovered. These include the human remains from the Pine Harbor site (100–200 individuals), Santa Catalina de Guale de Santa Maria (180 individuals), and Santa Maria de Yamassee (100–150 individ-
uals). Pine Harbor is a nonmission site located on the mainland approximately 15 km west of St. Catherines Island. The human remains here appear to be from the early contact period (mid- to late-16th century), although there is a late prehistoric component (F. Cook, 1980, n.d., personal commun.). Santa Catalina de Guale de Santa Maria is located on Amelia Island (Florida) and appears to be the descendent population from St. Catherines Island (Hardin, 1986). The site dates to the period of 1686–1702 (Bushnell, 1987; Hardin, 1986; Larsen and Saunders, 1987; Saunders, 1988). Santa Maria de Yamasse is a mission locality on Amelia Island that served a refugee population from interior Georgia from 1675 to 1683 (Larsen and Saunders, 1987; Saunders, 1988). The human remains from all three sites are currently under investigation.

Despite the large recovery of human remains from Spanish Florida, our knowledge of the biological impact of contact on native populations is poor. With the exception of human remains from San Pedro y San Pablo de Patale (Storey, 1986), Nombre de Dios (Loucks, 1979; Larsen, personal obs.), Pine Harbor (F. Cook, 1980, n.d.; Hutchinson and Larsen, 1988), Santa Catalina de Guale de Santa Maria (Hardin, 1986; Larsen and Saunders, 1987; Saunders, 1988), and Santa Maria de Yamasse (Larsen and Saunders, 1987; Saunders, 1988), all burials have been reinterred and are unavailable for study. The program of investigation of human remains that is underway for the Santa Catalina de Guale series will, therefore, greatly add to the knowledge of contact period biological adaptation from this region.

THE PROBLEM

What can be said about the nature of European contact and its impact on native populations in Spanish Florida? Prior to the investigation of the human remains from Santa Catalina, only one study of a native cemetery skeletal sample had been reported. Based on the series recovered from the Apalachee mission, San Pedro y San Pablo de Patale, Storey (1986) suggested that native populations experienced an apparent marked improvement in health in comparison with late prehistoric populations in the region (see also discussion in Hann, 1988). Health improvements in the contact period were related, in part, to greater access to animal protein. This paradox of supposedly decaying environmental conditions (e.g., increased disease stress) and improved skeletal health has been noted by a number of investigators from other contact period series outside of La Florida (D. Cook, 1985). I suspect, and the papers in this volume verify, that there is no clear-cut picture of all positive or all negative changes. Rather, the postcontact adaptations are complex and deserve to be looked at in greater detail involving the close study of a range of skeletal markers of adaptation and change.

When I began the bioarchaeological investigations of the Santa Catalina de Guale skeletal series, I was primarily interested in what seemed to be a simple and straightforward problem with a corresponding simple and straightforward solution. That is, the Guale were clearly on the decline. Therefore, should not all skeletal indicators of health and lifestyle show parallel declines as well? As the project developed, however, the true complexity of the issue of adaptation and change in this particular setting has emerged. The following papers will report on a number of avenues of the investigation that help us to understand some of this complexity.

The literature on the effects of European contact on native populations focuses largely on the dramatic reductions in population size of the latter. By and large, these studies document the cause and effect relationship between epidemics involving Old World pathogens and population reduction (e.g., Dobyns, 1983; Ramenofsky, 1987; M. Smith, 1987; Thornton, 1987). Although the issue of population collapse during the early years of contact between native populations and European populations is certainly an important one, it is the intent of this volume to broaden the scope of research in contact period bioanthropology by examining some of the many other important facets of adaptation and change. This is not to say that population reduction is not an important issue. For the Guale experienced great declines in this regard (see above). What is emphasized here, however, is that because native populations on the Georgia coast were interacting with Europeans on a nearly uninterrupted basis for
some 120 years prior to their removal in the late 17th century, equally important to the issue of population reduction are questions relating to how these populations responded and adapted to great social, dietary, and behavioral changes representing some five or six generations. It is the study of these details within this specific regional setting that will ultimately provide for greater understanding of the mosaic of issues that comprise the story of adaptation and change during this very critical period of time.

The hard tissues, skeletal and dental, are remarkably sensitive to the environment. A variety of factors, including disease and diet, population mobility, and physical exercise and work, leave a collective signature on the skeleton that directly and indirectly reflects environmental circumstances throughout the lifetime of the individual and the population (see review in Larsen, 1987). By study of this cumulative record of life experiences, it is possible to view these remains as representative of functioning, living populations that are in the process of adapting to wholly new environmental circumstances during the periods before and after contact. In order to go beyond the rather limited question of population reduction and epidemics, we have chosen to focus on two broad themes in the present volume. First, we examine the overall quality of life as it is revealed in the study of disease, demography, environmental stress, and dietary quality. Second, we examine the implications of behavioral change as it is exhibited in bone form and function in the postcranial skeleton.

The following chapters represent areas that address particulars of the adaptation of native populations in coastal Georgia. In order to provide necessary background for understanding historic period biological change, a number of these contributions discuss important data on precontact ancestral populations.

The volume is organized as follows. Chapter 2, by M. L. Powell, focuses exclusively on the single largest late prehistoric, Mississippian period population recovered by the Works Projects Administration during the late 1930s and early 1940s from the Irene Mound site. This skeletal series is important in that it represents the human remains from the dominant Mississippian ceremonial and habitation center in the region. As such, it provides material for understanding precontact infectious disease—treponematosis and tuberculosis—during the final centuries immediately preceding the arrival of Europeans. The remaining chapters focus primarily on the human remains recovered from Santa Catalina de Guale. Chapter 3, by K. F. Russell, I. Choi, and C. S. Larsen, outlines the demographic profiles of the premission and mission populations. In Chapter 4, D. L. Hutchinson and C. S. Larsen examine the evidence of environmental stress by study of enamel defects in teeth. This is followed by a discussion of preadult/adult differences in tooth size and enamel defects in Chapter 5 by S. W. Simpson, D. L. Hutchinson, and C. S. Larsen. M. J. Schoeninger, N. J. van der Merwe, K. Moore, J. Lee-Thorpe, and C. S. Larsen present findings on bone isotopic ratios (carbon and nitrogen) and evidence for dietary change in Chapter 6. Chapter 7 (C. B. Ruff and C. S. Larsen) and Chapter 8 (A. Fresia, C. B. Ruff, and C. S. Larsen) present findings on mechanical properties of long bones in order to reconstruct behavioral and work patterns before and during the contact period.

The chapters examine changes relating to three specific periods of time. The periods include (1) precontact preagricultural (pre-A.D. 1150); (2) precontact agricultural (A.D. 1150–1550); and (3) contact (A.D. 1607–1680). The first period restricts itself to those populations practicing a combination of hunting, gathering, and fishing prior to the Mississippian period. Little, if any, plant domesticates appear to have been important in the dietary regime. The second period includes those populations that practiced agriculture in addition to continuation of hunting, gathering, and fishing. This period corresponds with the Mississippian period. The third and final period includes the population recovered from Santa Catalina de Guale on St. Catherines Island. This period is associated with a reorientation of native subsistence economy that continued to utilize maize agriculture. A more specific discussion of chronology of the Georgia coast can be found in Thomas et al. (1978), Thomas and Larsen (1979), and Larsen (1982).
ACKNOWLEDGMENTS

With the exception of Chapter 5, earlier versions of all chapters in this volume were originally presented as papers in a symposium organized by me for the annual meetings of the American Association of Physical Anthropologists held in New York City in 1987. An earlier version of Chapter 5 (S. W. Simpson, D. L. Hutchinson, and C. S. Larsen) was presented at the 1986 A.A.P.A. and Paleopathology Association meetings in Albuquerque, New Mexico.

This research would not have been possible without funding from the Edward John Noble and St. Catherines Island Foundations for the excavation of the Santa Catalina de Guale human remains during the years 1982 to 1986. I especially express my gratitude to Mr. and Mrs. Frank Y. Larkin for their support and encouragement. The American Museum of Natural History Undergraduate/Graduate Research Participation Program provided partial funding for field assistants.

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Numerous bioarchaeological crews deserve special thanks for working with me on St. Catherines, sometimes under very trying field conditions. I thank the following individuals for their very special efforts: Ms. Inui Choi, Mr. Robert E. Cochrane, Mr. Lauren Cook, Ms. Carolyn Craig, Ms. Nancy Demytenaere, Ms. Dianna Doucette, Ms. Janice Elliot, Mr. Marc Frank, Ms. Marjorie Horne, Mr. Dale L. Hutchinson, Mr. Eric Ingbar, Ms. Frances Keefer, Dr. Robert L. Kelly, Mr. Paul P. Kreisa, Mr. Tormod Kristensen, Ms. Michelle Lapointe, Ms. Deborah Marc Aurelle, Dr. J. Alan May, Ms. Jacqueline McDowell, Mr. Christopher Messier, Ms. Felice Mueller, Ms. Deborah Mayer O'Brien, Mr. Dennis O'Brien, Mr. Greg Paulk, Ms. Debra Peter, Ms. Carolyn Plesia, Mr. Benjamin Resnick, Ms. Sherry Riley, Ms. Tracey Roy, Ms. Katherine F. Russell, Ms. Mary Shotwell, Ms. Susan Simmons, Mr. Scott W. Simpson, Mr. David Skinas, Ms. Martha A. Terry, and Ms. Karen Jo Walker.

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A rich record of written documentation from the 16th and 17th centuries for Spanish Florida has been studied by a number of authorities. Two of these authorities—Dr. John H. Hann and Dr. Amy Turner Bushnell—shared translations and provided me with advice on a number of issues directly related to this project.

The figure artwork was prepared by Mr. Dennis O'Brien, Ms. Fran Keefer, Ms. Lisa L. Gosciejew, and Ms. Prisca Kolkowski. The photographs in Chapters 3 and 4 were taken by Mr. Barry Stark.

Detailed reviews of the entire manuscript by Dr. Patricia S. Bridges and Dr. David N. Dickel are especially appreciated. Both individuals provided numerous suggestions that have contributed to the clarity and accuracy of each of the chapters.

The fieldwork, research, and writing that went into the preparation of this volume occurred while I was on the faculty in the Department of Anthropology at Northern Illinois University. I thank that institution and my friends and colleagues there for support of these efforts.

The project is part of an interdisciplinary research program involving the study of many different aspects of the society, culture, and biology of a long extinct population that once inhabited the Georgia coast and St. Catherines Island. I thank my colleagues who contributed to the production of this volume and helped to make possible the detailed exploration of a little known area of inquiry that I believe offers new and important insight into a very critical period of human adaptation and change.
CHAPTER 2. ON THE EVE OF THE CONQUEST: LIFE AND DEATH AT IRENE MOUND, GEORGIA

MARY LUCAS POWELL

ABSTRACT

This chapter focuses on the Irene Mound site, a Mississippian period (A.D. 1150–1450) mortuary locality on the north Georgia coast. Differential diagnosis of abundant skeletal pathology in the Irene series revealed the presence of two diseases of radically different morbid and mortal effects, namely treponematosis and tuberculosis. The former disease produced widespread inflammatory response localized in the lower legs and arms, with few cranial and nasal-palatal lesions. The demographic and pathological features of its manifestation point to endemic maintenance rather than venereal transmission. By contrast, the latter disease was far less visible, and is evidenced by rib lesions with only occasional vertebral and hip involvement. The identification of these diseases, previously documented elsewhere in the precontact southeastern United States, provides an important epidemiological baseline for studies of health in contact-period populations on the Georgia coast.

INTRODUCTION

In a broad-scale analysis of diachronic changes in health among aboriginal peoples of the Georgia coast, Larsen (1982) documented significant reductions in skeletal and dental dimensions and increased rates of dental caries and skeletal infection in prehistoric agriculturalists relative to their nonagricultural predecessors. The present study focuses on the largest population sample in the series, namely the precontact agricultural community at the Irene Mound site. The Irene Mound site, located near the mouth of the Savannah River just north of the city of Savannah on the north Georgia coast, was occupied from approximately A.D. 1150 to 1450 during the Savannah and early Irene phases, the regional expressions of the Mississippian cultural tradition (Caldwell and McCann, 1941; Larsen, 1982). Archaeological excavations supported by the Works Projects Administration from 1937 to 1940 recovered 265 burials, representing 280 individuals, from this locality.

The secular decline in body size and the dental evidence for a high-carbohydrate diet notwithstanding, other skeletal indicators suggest that nutrition in the Irene Mound population was generally adequate and that infection by endemic diseases was typically met with vigorous immune response. In particular, there is a low prevalence of porotic hyperostosis and cribra orbitalia (Powell, unpubl.), suggesting that severe chronic hemolytic anemia was not a major health problem (Ortner and Putschar, 1985; Steinbock, 1976), despite the use of iron-poor foods—especially maize—in the Irene Mound diet and the intensive occupation of a restricted village area conducive to the continual exchange of endemic pathogens and contamination by fecal wastes (see also discussion in Larsen, 1987, for alternative explanation).

Of the 109 crania in the series that were suitable for examination for porotic hyperostosis and cribra orbitalia, only one young adult female (20–30 years) displayed a few remodeled lesions characteristic of the former condition (0.9% prevalence). Nine individuals (8.3%), including this female, exhibited mild to moderate cribra orbitalia, all of which were at least partially remodeled. These individuals included two juveniles (10–15 years), two adolescents (16–20 years), two young female adults, two young male adults, and one old female adult (40–50). The overall prevalence rate is comparable with rates reported for other late-prehistoric eastern United States series: for example, 6 percent at Kane Mounds (Milner, 1982); 6.9 percent at Lubub Creek (Powell, 1983); 8.2 percent at Hardin Village (Cassidy, 1984); and 9.3 percent at Moundville (Powell, 1988). However, the lack of young preadult cases in the Irene Mound series differs from the age-graded prevalence patterns in these other series: for example, 50 percent of the Kane Mounds preadult cases aged three years or younger,
and six of the 10 (60%) Moundville preadult cases aged one to five years. This discrepancy seems most likely due to sample bias with regard to young Irene Mound preadults represented by the appropriate cranial elements.

As is the case for the entire precontact sample (see Russell et al., this volume), infants and older juveniles are underrepresented in the Irene Mound series. Despite this problem, preadult mortality assumes the expected profile: that is, there is a decline in deaths after age five until late adolescence (cf. Weiss, 1973). The modal age-at-death for adults was 30 to 35 years. Male mortality peaked sharply during the modal period (an increase from 9% for males in their late twenties) to 25 percent. This age profile suggests that there is an age-related increase in exposure to a variety of dangers, including, for example, those associated with warfare and hunting. By contrast, female mortality was more equitably distributed throughout the third and fourth decades of life, suggesting a fairly steady risk rate during the prime child-bearing years.

In the aforementioned study by Larsen (1982), skeletal infections were not differentially diagnosed as to specific etiology. However, follow-up differential diagnosis (this investigation) revealed the presence of endemic treponematosis and tuberculosis, two infectious diseases of radically different morbid and mortal effects (see discussion below). The identification of these diseases at Irene Mound forms part of an ongoing assessment of the social and biological dimensions of health in that community. On a regional level, it adds to a growing body of data documenting pre-Columbian treponemal disease and tuberculosis in the eastern United States from a variety of contexts: Alabama (Powell, 1983, 1988, in press), Arkansas (Powell, 1989), Tennessee (Jones, 1876; Widmer and Perzigian, 1981; Kelley and Eisenberg, 1987), Louisiana (Robbins, 1978), North Carolina (Reichs, 1989), Florida (Bullen, 1972, 1973; Iscan and Miller-Shaivitz, 1985), the central Ohio River Valley (Katzenberg, 1976; Widmer and Perzigian, 1981; Perzigian et al., 1984; Cassidy, 1984), and the central and lower Illinois River Valley (Buikstra and Cook, 1980, 1981; D. Cook, 1980; Milner et al., 1988; Milner and Smith, n.d.) (and see discussions in Buikstra, 1981; Clark et al., 1987; Baker and Armelagos, 1988).

The importance of infectious disease as a selective force in human adaptation has been argued during the past quarter century (e.g., Alland, 1970; Armelagos et al., 1978). Ortner and Putschar (1985: 105) emphasized that "... infectious conditions affecting the skeleton tend to be subacute, chronic diseases and may not be the immediate cause of death." In fact, because bone lesions typically develop relatively late in the progress of disease following considerable soft tissue involvement, their presence is indicative of long-term immune response to infection. Some chronic diseases, such as endemic treponematosis, produce abundant skeletal morbidity, yet rarely result in death because of the nature of their pathophysiological effects (Robbins and Cotran, 1980; Hackett, 1951). For other chronic diseases, the reverse is true: tuberculosis often kills its hosts before any bone involvement develops.

The purpose of this paper is to describe the skeletal lesions that are diagnostic of each disease as they appear in the Irene Mound series and discuss the contrasting potential of the two diseases for impacting morbidity and mortality. In the concluding section, I discuss the implications of the precontact infectious disease experience for the Georgia coastal populations exposed to Old World pathogens introduced by the Spanish in the 16th century.

**ENDEMIC TREPONEMATOsis AND TUBERCULOSIS**

The modern diseases included under the collective name "treponematosis" that leave their mark upon the human skeleton are yaws, nonvenereal syphilis, and venereal syphilis (Hackett, 1976; Hudson, 1958; Ortner and Putschar, 1985; Steinbock, 1976). They are considered to be closely related because of the similarity of their causal pathogens (bacterial spirochetes of the genus *Treponema*) and their lesion morphology. Steinbock (1976: 91–92) has commented in this regard:

In man, partial cross-immunity exists between syphilis (both nonvenereal and venereal), yaws, and pinta ... all pathological differences are merely quantitative with considerable overlapping between the syndromes. ... [A] pathological gradient [exists] extending from the cutaneous manifestations of pinta to the ulcers of
yaws involving both skin and bone, to similar lesions of endemic syphilis affecting the skin, bone, and cardiovascular system, and finally to the lesions of venereal syphilis affecting all of the organs just mentioned in addition to the nervous system.

The first two syndromes are typically contracted in early childhood through nonvenereal contact with infectious skin lesions, and are both more widely prevalent in endemic contexts and less life-threatening in the pathophysiological effects. Unlike venereal syphilis, they rarely dampen fertility levels or directly cause death, although secondary bacterial or mycotic infections may prove fatal.

Tuberculosis is a chronic disease caused by *Mycobacterium tuberculosis* and closely related spp. In situations where tuberculosis is endemic, most people are exposed in infancy or childhood, but pathological symptoms appear in less than half of the exposed but otherwise healthy individuals (Myers, 1951). (This relatively low prevalence of clinical disease contrasts sharply with the near 100% prevalence of symptoms in individuals exposed to treponematosis [Robbins and Cotran, 1980].) Individuals with poor immune response may develop primary lesions within the lungs and hilar lymph nodes. In those individuals who survive the initial illness, the pathogens are gradually encapsulated by calcified tissue within the lungs. This response halts the immediate progression of the disease, but the pathogens may remain viable for decades. If the infected person is reinfected or experiences severe systemic stress later in life, then the capsules may rupture and spread mycobacteria via direct or hematogenous dissemination throughout the body, thus producing acute pathological symptoms decades after the original exposure. Such cases are actively infectious, and enable the disease to be maintained through successive generations even in small population groups (Myers, 1951).

Table 2-1 summarizes the contrasting morbid and mortal effects of endemic treponematosi and tuberculosis in human populations. These different patterns have important implications for the paleopathological identification of these diseases in archaeological skeletal series. Endemic tuberculosis is less “visible” than treponematosi because it typically produces clinical symptoms in proportionately fewer individuals and bone lesions in relatively few of those who do fall ill. The osteolytic lesions of tuberculosis tend to weaken the affected bones by diminishing their mass, whereas the osteoblastic reaction to endemic treponematosi increases bone mass, most typically in long bone shafts. The spinal elements (thoracic and lumbar vertebrae) which present the most readily identifiable lesions of tuberculosis tend to be underrepresented in many older archaeological skeletal series in museum collections because they were less systematically collected, in part due to poor preservation. For example, in the Irene Mound series, only 176 individuals out of 235 examined (75%) were represented by these vertebrae or ribs or both.

**ENDEMIC CHRONIC INFECTIOUS DISEASE AT IRENE MOUND**

A diagnosis of endemic treponematosi in the Irene Mound skeletal series was first suggested by frequent observations of periostitis on long bone shafts, particularly the tibia, fibula, radius, and ulna. This pattern matched that described by Hackett (1951) in yaws victims in Uganda as resulting from the recurrent episodes of periosteal inflammation in the late secondary and tertiary stages of that disease. Many tibiae from Irene Mound show areas of localized apposition, most typically on the lateral aspect of the anterior crest. Others display more extensive pathological involvement (fig. 2-1) approaching the classic deformity known in modern treponemal cases as “sabre shins.” Almost all cases from Irene Mound display remodeling that is indicative of extensive healing and quiescence of the disease prior to death, a feature also characteristic of endemic yaws and nonvenereal syphilis.

Another characteristic lesion of late-stage treponemal disease observed in the Irene Mound series is a distinctive type of cranial lesion resulting from gummatous ulcers which often develop on the scalp, arms, and legs (Hackett, 1951; Orner and Putschar, 1985). These ulcers are not innately pyogenic, but are vulnerable to superinfection by opportunistic organisms such as endogenous staph-
TABLE 2-1
Tuberculosis and Endemic Treponematosis: A Comparison of Morbid and Mortal Effects

<table>
<thead>
<tr>
<th></th>
<th>Tuberculosis</th>
<th>Treponematosis</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Epidemiology</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Pathogen</strong></td>
<td><em>Mycobacterium tuberculosis</em> and closely related spp.</td>
<td><em>Treponema pallidum, Treponema pertenue</em></td>
</tr>
<tr>
<td><strong>Mode of infection</strong></td>
<td>Respiration, ingestion</td>
<td>Skin lesions</td>
</tr>
<tr>
<td><strong>Modal age at exposure</strong></td>
<td>Childhood</td>
<td>Childhood</td>
</tr>
<tr>
<td><strong>Modal age at onset of disease</strong></td>
<td>Late adolescence, early adulthood</td>
<td>Childhood</td>
</tr>
<tr>
<td><strong>Duration of infectious state</strong></td>
<td>Decades (with latent periods)</td>
<td>5-10 years</td>
</tr>
<tr>
<td><strong>Pathology</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Initial lesions</strong></td>
<td>Lungs, hilar lymph nodes</td>
<td>Mucocutaneous tissues</td>
</tr>
<tr>
<td><strong>Subsequent lesions</strong></td>
<td>Any organ system</td>
<td>Mucocutaneous tissues, bone</td>
</tr>
<tr>
<td><strong>Prevalence of disease in endemic contexts</strong></td>
<td>10-50% of exposed individuals</td>
<td>&gt;75% of exposed individuals</td>
</tr>
<tr>
<td><strong>Radiographic prevalence of bone lesions</strong></td>
<td>3-7% of cases</td>
<td>5-15% of cases</td>
</tr>
<tr>
<td><strong>Predominant skeletal response</strong></td>
<td>Major: osteolytic; minor: osteoblastic</td>
<td>Major: osteoblastic; minor: osteolytic</td>
</tr>
<tr>
<td><strong>Potential for mortal effect</strong></td>
<td>Moderate to high</td>
<td>Low</td>
</tr>
</tbody>
</table>


Y. lokocci and pathogenic fungi (Ortner and Putschar, 1985). Gummatous ulcers frequently infect the underlying bone, producing the pathognomonic osteolytic lesions known as “caries sicca” (Hackett, 1976).

Irene Mound cranial lesions of this type are neither large nor extensive, and all cases show considerable remodeling before death. Posterior cranial vault lesions (fig. 2-2) often show more clearly than anterior vault (frontal) lesions the characteristic stellate configuration of the healed scar.

The mucocutaneous and osseous tissues of the nasal and oral cavities are also common sites of treponemal pathology. In a young adult female from Irene Mound with remodeled frontal scars, osteolytic lesions penetrated the palate and maxilla, with extensive remodeling of the right border of her nasal aperture (fig. 2-3). This form of facial involvement is known as “gangosa,” a Spanish word referring to the harsh nasal quality of the victim’s voice (Hudson, 1958).

Accounts of disease in native populations by European explorers and others provide important insights that complement skeletal evidence of particular paleopathological conditions. In *A New Voyage to Carolina*, published in London in 1709, the Englishman John Lawson described ailments that resemble endemic treponematosis among the Santee Indians, located some 200 miles to the north of Irene Mound. He wrote,

... they have a sort of Rheumatism or Burning of the Limbs, which tortures them grievously, at which times their legs are so hot, that they employ the young People continually to pour water down them... (and)... another Distemper, which is, in some respects, like the Pox, but is attended with no Gonorrhea. This not seldom bereaves them of their Nose. I have seen three or four of them render’d most miserable Spectacles by this Distemper. Yet, when they have been so negligent, as to let it run on so far without curbing of it; at last, they make shift to patch themselves up, and live for many years after; and such men commonly turn Doctors (Lawson, 1709: 223).

The Santee made a clear distinction between precontact and contact-period diseases. Lawson indicated that

... the Natives of America have for many Ages (by their own Confession) been afflicted with a Distemper much like the *Lues Venerea*, which hath all the Symptoms of the Pox, being different in this only: for I never could learn, that this Country-Distemper, or Yawes, is begun or con-
Fig. 2-1. Pathological modifications of Irene Mound tibiae associated with treponematosis. The tibia shown in the middle is non-pathological.

continued with a Gonorrhea; yet is attended with nocturnal Pains in the limbs, and commonly makes such a Progress, as to vent Part of the matter by Botches, and several Ulcers in the Body, and other Parts; oftentimes Death ensuing. I have known mercurial Unguents and remedies work a Cure, following the same methods as in the Pox... (1709: 18).
The symptom described by Lawson as "Rheumatism" and "nocturnal pains in the limbs" corresponds well with the episodes of ostalgia (deep bone pain) that afflict advanced cases of endemic treponematosis. The ulceration and deterioration of nasal structures, the absence of urethral discharge ("gonorrhea"), the responsiveness of the skin lesions to "mercurial Unguents and Remedies," and the predominantly self-limiting nature of the ailments are also prominent characteristics of that disease. Lawson noted that some victims of the "Country-Distemper" died from illness, but others survived despite severe facial disfigurement. The majority of Irene Mound individuals with treponemal bone lesions show relatively minor osseous changes, and when alive probably would not have appeared diseased to a casual observer of the 16th century. Most lesions were extensively remodeled by the time of death, and only a few cases were widespread in the body and clearly active at the time of death. No mortality effect was evident in a comparison of mean age-at-death for moderate to severe cases (almost all of them quiescent at death) and for adults in the sample as a whole. This pattern of demographic and skeletal involvement matches closely the pattern reported in a recent study of the contemporaneous Mississippian population at Moundville in Alabama (Powell, 1988, in press).

Lawson commented that the Santee were "never troubled with the "Scurvy, Dropsy, nor Stone," and that "they are wholly Strangers to . . . the Phthisick, Asthma, and Diabetes." The term "Phthisick" refers to pulmonary tuberculosis (Jaffe, 1972: 955). Although it may have been absent among the Santee, skeletal evidence clearly indicates that tuberculosis was present in the Irene Mound population. Three individuals exhibit osteolytic lesions in thoracic or lumbar vertebrae characteristic of spinal tuberculosis (Pott’s disease) (see descriptions in Ortner and Putschar, 1985; Steinbock, 1976). The second through the fifth lumbar vertebrae of one of these young adults—a female—displays extensive shallow lesions on the paradiscal surfaces (fig. 2-4). The third and fourth thoracic
Fig. 2-3. Irene Mound maxillary pathological modifications associated with treponematosis.

Fig. 2-4. Irene Mound vertebrae showing pathological modifications associated with tuberculosis.
Vertebral bodies are by far the most common loci of tuberculosis skeletal lesions reported in clinical cases (Ortner and Putschar, 1985). This is followed in frequency by the knee and the hip joints. Tuberculous lesions were identified in neither the knee nor the hip joints in the Irene Mound series, but several other loci were clearly affected. One older adult female displayed extensive destruction of the left sacroiliac auricular surface with minimal remodeling (fig. 2-5). Two individuals displayed periostitis on the pleural aspect of the scapula, and the pleural aspect of the sternum was also similarly affected in one individual.

The most commonly observed extravertebral skeletal lesions characteristic of tubercular infection were those affecting the pleural aspects of ribs. These rib lesions were present in 8 of the 10 cases (10/176, 5.7%) initially identified by other lesions. In one case, focal osteolytic lesions were surrounded by osteoblastic response. Seven of the eight displayed localized or diffused subperiosteal apposition. Figure 2-6 shows the most extreme case with rib involvement. This individual, a young female adult, also exhibited multiple lumbar paradiscal lesions.

Kelley and Micozzi (1984) have indicated that in early 20th century clinical cases, the formation of rib lesions from direct contact with diseased tuberculous pleural tissues had been reported. But the prevalence of the bone lesions was believed to be quite low (between 3 and 7%) because they were seldom observed radiographically or in autopsy samples. These researchers examined skeletal lesions in clinically diagnosed tuberculosis cases in the Hamann-Todd skeletal collection, and reported that direct observation of dry bone specimens indicated a much higher prevalence rate. They noted that "more than half (56%) of all individuals with tuberculosis
skeletal lesions in the Hamann-Todd collection displayed rib lesions” (1984: 385). These rib lesions rarely appeared in individuals who displayed extrathoracic (e.g., hip) lesions.

There are two broad categories of tubercular infections. The first category represents direct osseous involvement from chronic pulmonary disease, and the second results from hematogenous spread of tuberculosis bacilli throughout the body. Because chronic pulmonary tuberculosis comprises approximately 90 percent of human cases of the disease (Kelley and Micozzi, 1984), rib lesions are more likely to occur than are nonthoracic lesions of the hip and the knee. Paleopathological investigations of tuberculosis have been significantly facilitated by this emphasis upon newly recognized skeletal evidence of the chronic “smoldering” form of the disease. Rib lesions are less dramatic in appearance than the spectacular spinal deformities of Pott’s disease or hip joint destruction, but their higher prevalence in infected populations increases the chances that they will be preserved and recognized in the archaeological record.

The great majority of the 80 individuals (80/235, 34%) from the Irene Mound site that displayed distinctively treponemal bone lesions were adults aged 30 years or older at death. By contrast, the mean age-at-death of the 10 individuals with characteristic vertebral, pelvic, and rib lesions of tuberculosis was 29.5 years, five years below the modal sample age of 34.9 years. One young adolescent, one older adolescent, and four adults aged 20 to 24.9 years comprised the younger set of cases. Approximately 15 years separated the oldest of these cases from the youngest of the four remaining cases. All of these individuals were in their early to late 40s. There were twice as many female as male cases, in contrast to the equal representation of the sexes in the Moundville skeletal sample (cf. Powell, 1988, in press).

**IMPLICATIONS OF PRECONTACT INFECTIOUS DISEASE EXPERIENCE FOR POPULATION RESPONSE TO INTRODUCED OLD WORLD PATHOGENS**

What implications did precontact aboriginal experience with endemic New World forms of treponematosis and tuberculosis have for population response to introduced Old World variants of these diseases? Hackett (1951, 1976) and Hudson (1958) have discussed the question of mutual cross-immunity conferred by the different treponemal syndromes. Some positive degree of immunity may be conferred against new doses of pathogens of the same or different strain by previous infection acquired in early childhood, but the strength of this protection is quite variable. Reinfection of healed cases or superinfection of latent cases may create serious health problems in previously exposed
individuals. Reactivation of an inappropriately vigorous allergic response from previously sensitized tissues may result in destructive tertiary gummatous and osteoperiostitic lesions (Grin, 1956: 969).

Between 75 and 80 percent of new clinical cases of tuberculosis are considered to represent flare-ups of previously acquired infection that had been effectively immobilized by vigorous immune system response (Hepprich, 1977: 323; Robbins and Cotran, 1980: 397). Reinfection or superinfection in adult life of previously sensitized individuals, particularly those experiencing the multiple physical and psychological stresses associated with catastrophic cultural disruption, may result in seriously detrimental physiological reactions (Jaffe, 1972: 955). It has been suggested that prolonged exposure to certain environmental mycobacteria such as M. kansasii and M. intracellulare may confer some degree of heightened resistance—possibly through acquired cellular immunity—to infection by M. tuberculosis. But, the exact nature and extent of this hypothesized protection has not been determined (Youmans et al., 1980).

A population’s past experience with a particular infectious disease may, in some cases, confer a collective genetic advantage against newly introduced strains of the disease through the long-term process of “weeding out” susceptible genotypes. Moreover, for diseases like smallpox and measles that do not confer lasting individual immunity, previous population exposure is clearly advantageous in the face of a new wave of infection. However, for chronic infectious diseases that do not confer lasting immunity, such as tuberculosis and treponematosis, the degree of population exposure to the New World variants on the eve of the conquest may well have exacerbated individual responses to Old World variants at the time of contact.

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CHAPTER 3. THE PALEODEMOGRAPHY OF SANTA CATALINA DE GUALE

KATHERINE F. RUSSELL, INUI CHOI, AND CLARK SPENCER LARSEN

ABSTRACT

The purpose of this chapter is to outline change in demographic profiles—survivorship, mortality, and probability of dying—of native populations occupying the Georgia coast, both before and after contact. This study is based on comparisons of precontact preagricultural (N = 147), precontact agricultural (N = 142), and contact (N = 292) period individuals. Ages were determined primarily by the Miles (1963) method based on functional dental wear of occlusal surfaces of teeth.

Comparison of demographic profiles shows a number of differences between the three periods. Most outstanding in this regard is a greater survivorship for the contact period Santa Catalina de Guale population in comparison with the precontact agricultural period. This finding suggests that either the contact period population experienced a rebound in health or certain segments of the population were not included in the burial sample, thereby biasing the age profiles. The influence of population growth and fertility is also considered. Population size for the contact period sample from St. Catherines Island is estimated at 125 to 132 individuals. The clear underenumeration of juveniles in the death sample suggests that this is a very conservative estimate.

These results do not produce the expected demographic parameters of a living population, nor are the assumptions necessary for producing comparative life tables fulfilled. The data presented in this study should, therefore, be interpreted in light of these limitations.

INTRODUCTION

The human remains recovered at Santa Catalina de Gaule offer a unique opportunity to study the consequences, both direct and indirect, of the arrival of the Spanish on the native populations of the Georgia coast. A comprehensive understanding of the prehistoric subsistence, lifeways, and human biological adaptation provides the basis for assessing diachronic changes in lifeway and health in a controlled cultural and geographical area.

This chapter utilizes some primary paleodemographic variables to investigate the relative quality of life and health status of the precontact preagricultural, precontact agricultural, and contact Guale from St. Catherines Island and the mainland. This approach to the study of lifeway has been recognized by a number of scholars in elucidating the relative success of human populations (cf. Buikstra and Mielke, 1985).

The overall decline in health and increase in environmental stress with the adoption of agriculture worldwide has been noted by a number of workers (see various studies in Cohen and Armelagos, 1984). The term "stress" is used to denote the diverting of essential nutrients from bone growth to more immediate tissue maintenance due to disease and nutritional deprivation. Stressors, on the other hand, represent an amorphous group of physical, physiological, and psychological variables that reflect the individual's interaction with his environment. Although the increase or decrease in stress indicators in bones and teeth can be measured to assess the relative health of the population (Goodman et al., 1984; Larsen, 1987), the level at which these stressors produce identifiable results on the hard tissues is not easily measured.

If the cumulative effect of stressors acting on an individual are severe enough, death results. Therefore, at the population level, stressors acting on individuals can result in changes in demographic profiles in a skeletal sample representing a population. Paleodemography draws directly from the percent of the sample in each five-year age category (called mortality here), and provides one gross measurable indicator of stress.

Ethnohistoric evidence suggests that the Guale suffered an onslaught of new and intensified stressors during the Spanish contact period. The Guale were forced to cope with Spanish tax and tribute demands, religious
and cultural conversion, and a new host of infectious diseases to which they had no acquired immunities (see Larsen, this volume). In the skeletal record, these demands on health should be recorded as increased population-level stress exhibited on the hard tissues and in a shift toward higher preadult and earlier adult mortality. The change in distribution of mortality and how the change translates into survivorship and probability of dying are the foci of this analysis.

It appears that the model of a continual decrease in the quality of health as a result of European contact on the Georgia coast is much too simplistic. Although the Guale certainly suffered the effects of new and intense stressors during the contact period, the severity, consistency, and measurability of these stressors are not as yet clear from paleodemographic analysis.

AGE DETERMINATION

Paleodemography requires consistent and accurate age estimation for each individual studied in a skeletal sample (Ubelaker, 1974; Buikstra and Mielke, 1985). Whether or not accurate age assignments or meaningful age profiles of a sample population can be made from an archaeological context has been the focus of considerable debate (Angel, 1969; Bocquet-Appel and Masset, 1982; Buikstra and Koningsberg, 1985; Van Gerven and Armelagos, 1983; and others). It is our contention that when care is taken to systematically determine age for each individual and all potential archaeological, cultural, and preservation biases in the sample are considered, then paleodemography can be a useful tool in assessing diachronic changes in population stress over time.

The method used in this study for assigning dental age is a modified version of the method of functional dental wear developed by A. E. W. Miles (1962, 1963, 1978). The Miles method has the unique advantage over many other age indicators in that it is specifically tailored for each population to which it is applied. We have chosen the Miles approach to dental aging because the precontact and contact Georgia coastal dental remains are far more numerous and better preserved than other areas of the skeleton that have been used for aging purposes by physical anthropologists (Ubelaker, 1984; Molleson, 1986). The Miles method is based on the premise that the first permanent molar (M1) will average six more years of wear on it than the second permanent molar (M2). Likewise, the M2, will have six more years of wear than the third permanent molar (M3). Miles first developed the aging technique by examination of 157 Anglo-Saxon skeletons from Breedon-on-the-Hill in Leicestershire, England (Miles, 1963). Thirty-eight juveniles in the sample were aged using dental eruption and calcification standards. Miles then seriated the preadults from youngest to oldest and found that there was a consistent relationship between amount of occlusal wear and age. He proposed that the adults in his sample could be aged by employing this relationship between molar wear and age. He defined "functional age" of a molar as the number of years for which the molar had been in use. Therefore, Miles assigned a functional age to each molar based on the amount of wear it exhibited and then assigned a chronological age to each individual based on a synthesis of the functional ages for each of the teeth available.

A number of investigators have tested the accuracy of the Miles method. For example, Lovejoy (1985) successfully applied a modified Miles method to a sample of dentitions from the Libben site, Ohio. This investigator found that the separately seriated maxillary and mandibular ages were highly correlated, thereby indicating consistency in the application of the method. More importantly, dental wear consistently correlated highly with other reliable age indicators in a multifactorial scheme to establish age-at-death based on five independent indicators of skeletal age.

It might be argued that testing any method of skeletal aging by using individuals of "unknown" age-at-death does not help in assessing the accuracy of aging methods. A study by Keiser and co-workers (1983) helped to address this suspicion with respect to the accuracy of the Miles method. These investigators applied the Miles method to a living population of Lengua Indians from Paraguay and found that there were no statistical differences between the Miles subgroups and known ages in the Lengua subgroups. These
findings strongly suggest that the method is an accurate approach to age estimation.

In sum, based on the aforementioned studies by Lovejoy, Keiser and co-workers, and others (e.g., Costa, 1986; Nowell, 1978; Ruff, 1981; Sciuilli and Aument, 1987; Wolpoff, 1979), it appears that use of this approach to determine age-at-death is highly reliable.

Although dental wear provides a reliable single indicator of age-at-death in skeletal series, three considerations must be addressed. First, estimation of skeletal age should utilize as many independent indicators of age as are available. Because of the variable preservation of nondental human remains at Santa Catalina, we could not improve our age estimates with additional reliable indicators (e.g., pubic symphysis, auricular surface). Second, in order to use dental wear to estimate age, it must be assumed that the preadult age assignments based on dental calcification and eruption are correct. We can estimate with confidence the ages of preadults using a dental calcification and eruption scheme calibrated for Amerindian populations by Ubelaker (1984). Although rate and time of dental eruption may vary slightly with sex, race, nutrition, and deciduous exfoliation (Garn et al., 1959; Miles, 1978: 456; Moorrees et al., 1963), these variations present virtually no bias when preadults are grouped into five-year age classes.

Third, it must be assumed that there is a consistent wear pattern throughout life, and that the rate of wear for each tooth is independent of status, sex, and age. In prehistoric and early historic Amerindian skeletal samples, circumstances of life were certainly more homogeneous than for any modern sample. In an archaeological sample, such as any of the Georgia coast samples, the dental wear would be considerably more homogeneous than in modern industrial populations (e.g., Lovejoy et al., 1985). Assuming that the variation in tooth wear that might be associated with sex and social status is evenly distributed around a mean, then we are left to demonstrate that there is a consistent wear pattern independent of age.

All age schemes based on dental attrition assume that occlusal wear and chronological age have a linear relationship. The results of a limited test performed as part of this study (see also Choi, 1986; Costa and German, 1986; Russell, 1987) suggest that a linear model acts as the best general indicator of dental wear. This relationship is not strictly linear, however. During the seriation and analysis of the Santa Catalina dental sample, we recognized that there may not be a consistent wear pattern throughout life, and that the rate of wear may not be completely independent of age. It was our aim to determine if there was a directional error, and if so, could we systematically compensate for that error.

Miles detected a directional bias in rate of wear between the permanent first molar (M1), second molar (M2), and third (M3). Therefore, he assigned the 6.0:6.5:7.0 wear gradient to compensate for the M3 wearing slower than the M2 and the M2 wearing slower than the M1. Our examination of the Santa Catalina dentitions suggests that differences in wear rate between teeth might be due to both position of molar in masticatory load—position of M1 relative to M2, and M2 relative to M3—and functional age of the tooth. If both molar position and functional age holds true, then a consistent ratio may not represent the best description of functional occlusal wear.

In order to examine tooth position in relation to functional occlusal wear in more detail, we scored mandibular molar wear based on an ordinal system established by Smith (1984) for all individuals less than 19 years of age. The results were regressed against dental developmental ages (fig. 3-1).

Results from the regression analysis of the Santa Catalina sample are presented in table 3-1. When the mandibular M1 is carrying the complete posterior occlusal load, it takes 1.08 years to wear approximately one stage on the ordinal wear scale. When both the M1 and M2 are in occlusion, it takes 2.85 years for the same M1 to wear one stage. In essence, then, the rate of wear on the M1 slows down after the eruption of the M2. The rate of wear for the M2 is 2.13 years per stage which suggests that the M2 is wearing slower than the M1 did during the first years of its occlusion, yet faster than the M1 after the M2 erupts. These results suggest that there is clearly not a constant rate of wear for the molars through life and that there is some oscillation in the rates of wear.
Examining the complete sample of preadult molars shows that the years per wear stage for the M1 and M2 are 2.45 and 2.14, respectively. Therefore, over the range of years from ages 7 to 19, the rate of wear for the M2 is slightly faster than that exhibited for the M1 (contra Miles, 1963, and Murphy, 1959, but in agreement with Swärdstedt, 1966; see also Wolpoff, 1979) during this age period.

Although the regression analysis in table 3-1 shows that there may not be a constant rate of wear, it may itself be partly clouded by the problem of scoring wear on an ordinal scale. Lunt (1978) suggested that most scoring techniques are biased toward scoring wear stages that are easy to recognize; the scoring scheme used here is certainly no exception.

For the present investigation, a 1:1:1 wear ratio was applied for the M1:M2:M3 instead of a 6.0:6.5:7.0 wear ratio. In the Santa Catalina sample, the rates of wear seem to vary more with age of the tooth than with molar type. Nowell (1978), who tested the accuracy of the Miles method using a sample of dentitions (120 adults, 19 preadults) from Tepe Hissar, Iran, also utilized a 1:1:1 ratio in lieu of the 6.0:6.5:7.0. Although the assumption that there is a positive and linear relationship between dental wear and age is the best model for describing dental wear, there are problems with it. On a population level, however, we argue that there is only limited directional error.

The Santa Catalina cemetery was completely excavated, producing human remains representing a minimum of 431 individuals. Of these individuals, 292 had teeth preserved well enough for determining dental age. Following the dental eruption and calcification schedule developed by Ubelaker (1984), we determined the ages for 122 preadults.

The remaining 170 adult individuals were aged by the above discussed Miles method of functional dental wear.

For an individual to be included in the Santa Catalina dental aging sample, at least three teeth had to be present, including at least one molar. All of the mandibular dentitions were seriated from youngest to oldest based on dental development and wear. The
maxillary dentitions were seriated separately using the same methodology. Preadults were aged first, based on calcification and eruption. In this study, "eruption" is defined as clinical eruption from the tooth crypt. The standards used include the following: The first permanent molar (M1) erupts from the crypt at six years of age and reaches functional occlusion at approximately seven years of age. Likewise, the M2 erupts from the crypt at approximately 12 years of age and reaches functional occlusion at 13 years of age. The first indication of occlusal surface wear facets is defined as evidence of a tooth having reached functional occlusion. Primary cusp removal is measurable after a molar has been in functional occlusion for one year. Table 3-2 outlines the scheme used for Santa Catalina dental development and functional age.

Regularity in the dental wear in the samples is evident. Overall, dental attrition is slow by prehistoric Native American standards, indicating a relatively soft and processed diet. Occlusal surface wear is generally slightly greater in the mandibular molars than the maxillary molars (see also Lovejoy, 1985; Molnar, 1971; Wolpoff, 1979). After about 40 years of age, the rate of wear accelerates and becomes erratic. There is a high frequency of impacted and diminished M3s in the Santa Catalina sample. This, of course, is not an uncommon phenomenon (Demisch and Wartmann, 1956; Garn et al., 1959; Smith, 1984; Swärdstedt, 1966). Therefore, the M3 was de-emphasized in the analysis of age. It is suspected that antemortem tooth loss was substantial in the fourth and fifth decades. However, the variable state of preservation of remains precludes us from assessing frequency of antemortem tooth loss in this series.

Adult dental ages were assigned by individual and modal comparisons of all available molars. For example, in figure 3-2, the molar wear for the mandibular M1, M2, and M3 are compared in two individuals—a 21 year old and a 27 year old. Usually three or more individuals of similar age (e.g., ages 20, 21, and 22) would be used to help assess the target age assignment of the 27 year old. Then, premolars and anterior teeth were used to refine relative position of teeth in seriation. Figure 3-3 shows the Santa Catalina seriated dentitions during analysis.

**PALEODEMOGRAPHY**

The primary purpose of this analysis is to utilize the assigned age estimates to assess the impact of European contact on the health and quality of life of the contact period native population occupying St. Catherines Island. For reasons outlined by Larsen (this volume), we anticipated that the Santa Catalina populations experienced a decrease in overall health status during the contact period.

A prehistoric transition from a hunting and gathering economy to an economy based at least partially on maize agriculture occurred on the Georgia coast during the 12th century.
Fig. 3-3. Seriated dentitions from Santa Catalina de Guale.
The change to a more sedentary agricultural existence suggested a trend toward decrease in health and nutrition during the precontact agricultural period compared to the precontact preagricultural period as measured by skeletal indicators of stress (Larsen, 1982).

The preagricultural and agricultural dental samples were aged separately by dental wear as part of an earlier study by Larsen (1982). The preagricultural sample consists of 272 individuals from 19 mortuary sites on the Georgia coast. It is limited to the 147 individuals aged by dental development and wear, 96 of whom are 20 years of age or older (table 3-3). Preagricultural diet included wild plants and animals, the latter of which were extracted primarily from marine resources. Nearly all of the preagricultural individuals collectively date from A.D. 500 to 1150.

The agricultural sample consists of 345 individuals from 14 mortuary sites. The precontact agricultural sample is limited to the 142 individuals aged by dental development and wear from the Irene Mound site on the north Georgia coast. Of these aged individuals, 67 are 20 years of age or older. Irene Mound makes up 90 percent of Larsen’s (1982) agricultural sample and dates primarily from A.D. 1150 to 1450.

Shortly before or during the initial occupation of the Irene Mound site, the settlement pattern and subsistence base underwent a general reorientation on the Georgia coast. Archaeological evidence suggests that a subsistence strategy shifted toward dependence on agriculture, particularly maize, but that the maize diet was supplemented to different degrees by traditional marine and terrestrial food sources (Larsen, this volume; Schoeninger et al., this volume). These later populations appeared to have been larger and generally more sedentary than the preagricultural populations.

The contact period sample from Santa Catalina de Guale consists of the 292 individuals who were aged by dental development and wear, 170 of whom were at least 20 years of age. These individuals are associated with a period of time during which there appears to have been more intensive use of maize agriculture and further nucleation of population (Larsen, this volume).

Number of deaths \( (D_i) \) and percent of deaths \( (d_i) \) for each age interval \( (x) \), and mean age-at-death for the precontact preagricultural, precontact agricultural, and contact samples are presented in table 3-4. These data indicate that the proportion of preadults in all three Georgia coast subsamples is alarmingly small. In the early Late Woodland Libben sample from Ohio, Lovejoy and co-

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**TABLE 3-3**

**Adult Individuals Aged by Dental Wear from Georgia Coastal Mortuary Sites**

<table>
<thead>
<tr>
<th>Temporal period/site</th>
<th>N</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precontact preagricultural</td>
<td></td>
<td></td>
</tr>
<tr>
<td>McLeod Mound</td>
<td>11</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Seaside Mound I</td>
<td>5</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Seaside Mound II</td>
<td>3</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Airport Site</td>
<td>18</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Deptford Site</td>
<td>16</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Cannons Point Site</td>
<td>9</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Sea Island Mound</td>
<td>11</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Johns Mound</td>
<td>16</td>
<td>Larsen and Thomas, 1982</td>
</tr>
<tr>
<td>Marys Mound</td>
<td>1</td>
<td>Larsen and Thomas, 1982</td>
</tr>
<tr>
<td>Charlie King Mound</td>
<td>3</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Cedar Grove Mound C</td>
<td>3</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Precontact agricultural</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Irene Mound Site</td>
<td>67</td>
<td>Caldwell and McCann, 1941</td>
</tr>
<tr>
<td>Contact</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Santa Catalina de Guale</td>
<td>170</td>
<td>Russell, 1987; Larsen, this volume</td>
</tr>
</tbody>
</table>
TABLE 3-4
Number of Individuals (D_i) and Mortality (d_i), in Age Classes, and Mean Age-at-Death

<table>
<thead>
<tr>
<th>Age (x)</th>
<th>D_i</th>
<th>D_x</th>
<th>d_i</th>
<th>d_x</th>
<th>D_x</th>
<th>d_x</th>
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<td>8.16</td>
<td>16</td>
<td>11.27</td>
<td>27</td>
<td>9.25</td>
</tr>
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<td>10.20</td>
<td>12</td>
<td>8.45</td>
<td>42</td>
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<td>22</td>
<td>14.97</td>
<td>36</td>
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<td>57</td>
<td>19.52</td>
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<tr>
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<td>11.56</td>
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<td>7.04</td>
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<td>7</td>
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<td>27</td>
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<td>2</td>
<td>1.41</td>
<td>9</td>
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<td>15.65</td>
<td>4</td>
<td>2.82</td>
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</table>

Mean age-at-death 26.1 19.7 21.2
Total aged 147 142 292
Total adults aged 96 67 170

TABLE 3-5
Life Table for the Precontact Preagricultural Adult Sample

<table>
<thead>
<tr>
<th>Age (x)</th>
<th>D_i</th>
<th>d_i</th>
<th>l_i</th>
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</thead>
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<td>0.2292</td>
</tr>
<tr>
<td>25</td>
<td>17</td>
<td>17.71</td>
<td>77.08</td>
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</tr>
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<td>14</td>
<td>14.58</td>
<td>59.37</td>
<td>0.2456</td>
</tr>
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<td>35</td>
<td>10</td>
<td>10.42</td>
<td>44.79</td>
<td>0.2326</td>
</tr>
<tr>
<td>40</td>
<td>10</td>
<td>10.42</td>
<td>34.37</td>
<td>0.3032</td>
</tr>
<tr>
<td>45</td>
<td>23</td>
<td>23.96</td>
<td>23.95</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

workers (1977) found mortality in the first five years of life to be 30.72 percent. The Bt-5 sample from Kentucky analyzed by Mensforth (1986) exhibited a similar mortality in the first five years (29.66%). Compared with ethnographic series, these mortality data suggest that both the Libben and Bt-5 populations represent healthy populations (cf. Lovejoy et al., 1977; Mensforth, 1986).

The contact period Santa Catalina sample, in which we would expect to find a higher infant and young preadult mortality than in the prehistoric Libben or Bt-5 sample, instead exhibits a suspiciously low mortality of 9.25 percent in the first five year age interval (table 3-4). This obvious sampling error is also evident in the precontact preagricultural and agricultural Georgia coastal samples where the mortality for the first five years is 8.16 and 11.27 percent, respectively. Study of age composition of precontact mortuary localities on St. Catherines Island suggests that infants were not included in the cemetery population (see Thomas and Larsen, 1979; Larsen and Thomas, 1986). This might explain, in part, the significant underenumeration of young juveniles in the two precontact subsamples. In the mission cemetery, given the change in burial ritual associated with the introduction of Western religion, we might anticipate that more infants would have been buried in the consecrated grounds. It appears that some proportion of infants and young children were buried in the church cemetery at Santa Catalina, including a number with presumably high status European and aboriginal artifacts. The majority of preadults, however, were either buried elsewhere, not buried at all, or interred in the church cemetery but not preserved well enough for identification or recovery.

Exclusion of a nonrandom portion of the population—such as preadults—has obvious negative consequences for demographic analysis (Mensforth, 1986; Moore et al., 1975; Ubelaker, 1974, 1984). When there is nonrandom sampling from the population, as in the case of the three Georgia coastal subsamples, it is unlikely that their respective age profiles approximate true biological populations in either composition or demographic trajectories. Without limiting the life tables to adults only (20+ years), it would be necessary to assume that the cultural and preservational biases acting against the recovery of preadults are the same in all three samples. Therefore, the life tables have been constructed for the three samples using only individuals 20 years of age-at-death or older. The life tables for the respective precontact preagricultural, precontact agricultural, and contact periods are presented in tables 3-5, 3-6, and 3-7. Although the life tables do not represent the population as a whole, they permit comparison of otherwise incomparable samples.

The survivorship curves for the three adult samples are presented in figure 3-4. Survivorship represents the percent of the original sample population surviving after each five-year age interval. The precontact preagricultural sample demonstrates higher survivor-
ship at all adult age categories than either the contact or agricultural samples. Survivorship for the Santa Catalina sample falls between the agricultural and preagricultural samples until 35–40 years when the Santa Catalina survivorship falls below the agricultural survivorship. All three adult survivorship curves are statistically different (Kolmogorov-Smirnov: \( p < 0.05 \)).

The contact period survivorship curve would suggest that there is some rebound in young adult survivorship compared to the agricultural sample. However, there are also fewer older adults in the contact sample than in the agricultural sample. It is possible that fewer older people survived in the contact sample than in the agricultural sample. Another explanation for this phenomenon is that we might be measuring a differential preservation of older adults in the two subsamples (Walker et al., 1988). That is, the relatively greater fragility, and hence poorer preservation, of the older adult skeletal remains than the younger adult skeletal remains may explain the smaller number of older individuals in the death sample. Another important factor to consider is the difference in preservation between mortuary sites. The preservation of human remains at the Irene Mound site is generally quite good (Larsen, personal obs.). The human remains at Santa Catalina de Guale, however, show variable preservation. A number of Santa Catalina individuals are represented by dental remains, only. In some instances, the posterior dentition is preserved, but the anterior dentition is not due to very harsh soil conditions. In our study of dental age in the Santa Catalina series, it was clear that after age 40, a great deal of posterior premortem tooth loss is present. These findings suggest that if the anterior dentition is not preserved and the posterior dentition was lost prior to death, then the individual would not have been included in the death sample for demographic analysis. This factor could quite likely have contributed to an underrepresentation of individuals in older five-year cohorts.

Given the dramatic changes in subsistence and living conditions through time on the Georgia coast, it is difficult to separate biological from archaeological factors that might affect age distribution represented in survivorship.

The mortality curves for the three Georgia coast samples are presented in figure 3-5. Unlike survivorship, which is a summary presentation, mortality represents the percentage of individuals dying in each five-year age interval. Especially noteworthy in these curves is the elevated mortality in the agricultural sample at 20 years of age followed by a relatively suppressed mortality in the remainder of the adult cohorts.

The relationship between precontact agricultural and contact period mortality appears influenced by the very high adult mortality in the 20 year old agricultural period category. The reasons for the high young adult mortality in the agricultural sample are unclear. We suspect that there is a higher young adult mortality at the relatively densely populated Irene Mound site, which forms the basis of the precontact agricultural demographic profiles. The high young adult mortality may be enhanced even further by mortality due to warfare. Our examination of the Irene Mound series indicates a greater number of adult females than males in the sample. This fewer number of males may reflect a loss of their numbers to warfare (see also discussion by Powell, this volume).

<table>
<thead>
<tr>
<th>TABLE 3-6</th>
<th></th>
<th></th>
<th></th>
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<tbody>
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<td>l_x</td>
<td>q_x</td>
</tr>
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<td>l_x</td>
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Probability of dying for the three samples is presented in figure 3-6. These data provide an index of age-specific mortality. A higher probability of dying in most adult age categories in the contact sample than in the preagricultural and agricultural samples is evident. The exception is the 20 year age interval in the agricultural sample which has a higher probability of dying than the preagricultural or contact period samples. Again, it is clear that there are factors (biological, cultural, or archaeological) suggesting higher mortality in early adulthood in the agricultural sample. The probability of dying in the agricultural sample is lower than in the contact sample after the original wave of early adult mortality. In the contact sample, by contrast, we observe a relatively lower adult mortality in the first adult age category. However, the probability of dying rises consistently and is higher for the contact sample over the rest of the adult age categories than either the preagricultural or the agricultural sample.

Assimilating all of the demographic data together suggests a number of possible interpretations. The clearest observation is the relatively high mortality of the young adults in the precontact agricultural sample. Although we cannot attribute exact cause to this high early mortality, it is likely that at least part of it is related to a complex of stressors associated with the sedentary, nucleated, agricultural Irene community.

Overall, the Santa Catalina sample exhibits
Fig. 3-5. Mortality for the precontact preagricultural, precontact agricultural, and contact adult samples.

Some rebound in adult survivorship compared to the precontact agricultural sample. One possible explanation is that the adjustment—either immunological or otherwise—to the sum effects of European contact had already reached an equilibrium prior to the deaths of individuals represented in the Santa Catalina cemetery. That is, if the biological trauma associated with newly introduced pathogens and reorientation of lifeway and subsistence was being successfully mitigated, then there should be a net increase in overall health during the contact period compared to the precontact agricultural period. It seems possible that the changes in survivorship profiles reflect this adjustment. Most of the human remains in the Santa Catalina cemetery represent post-1597 rebellion interments. The human population from the mission, therefore, represents one that has been exposed to Europeans for nearly a century. We suggest, then, that the presence of relatively more adults in the older age cohorts during the contact period represents an adjustment to stress.

It is possible that the older age distribution in the contact sample may simply represent a decrease in growth or fertility during this time. Johansson and Horowitz (1986) have argued that age-at-death has an inverse relationship to fertility. That is, a decline in
Fig. 3-6. Probability of dying for the precontact preagricultural, precontact agricultural, and contact samples.

Age-at-death may represent an increase in fertility, and hence, increase in population growth. Therefore, we can suggest that the decline in age-at-death (table 3-4) and older adult mortality in the precontact agricultural population relative to the preagricultural population may have represented increase in fertility and growth prior to contact (after Johansson and Horowitz, 1986; see also Buikstra et al., 1986, 1987). In the contact series discussed here, the increase in age-at-death and higher percentage of adults in older age intervals may represent a decrease in fertility and reduction in population growth. If this is true, then the population was clearly not adjusting to stressors, but rather, was in the process of declining. Intuitively, the latter interpretation seems most likely given the de-
gree of overall stress that these contact populations experienced (summarized in Larsen, this volume). Moreover, other workers have pointed out that ages derived from skeletal series provide more information about fertility than mortality (see Sattenspiel and Harpending, 1983; Milner et al., 1989). Therefore, the shape of the age distributions in these series might be interpreted in light of fertility (cf. Milner et al., 1989).

The other most likely explanation for the observed rebound in survivorship is related to cultural factors. In the case of a cultural bias, we can speculate that "epidemic" death is not represented in the cemetery. We might also consider that certain age, sex, or status categories were not buried in the mission cemetery, most notably preadults, and non-baptized (perhaps older) individuals. Until we know more about settlement patterns at Santa Catalina de Guaule and have data from other Spanish missions in which skeletal preservation is more consistent, we are left with these alternative explanations.

Powell (this volume) has provided evidence for presence of specific infectious diseases (treponema and tuberculosis) in late prehistoric populations on the Georgia coast. Study of skeletons shows that these populations most likely responded to these diseases in a robust fashion. It is important to examine the effects of European-introduced infectious diseases in the contact populations. Unfortunately, it is not possible to document skeletal evidence for most of these diseases from bones alone (cf. Ortner and Putschar, 1985). In addition, a large proportion of the Santa Catalina skeletal remains are poorly preserved, thus complicating further our ability to document the presence of disease, either specific or nonspecific, in these remains. For these reasons, it is virtually impossible to discuss the relationship between demography and disease. There are examples of periosteal inflammations in the series that appear very similar to the treponemal changes documented in Irene series by Powell (this volume) (Larsen, unpubl.), but given the poor preservation, actual percentages for various skeletal elements cannot be accurately determined except with regard to a rather limited subspecies from the site.

**POPULATION SIZE: SANTA CATALINA DE GUAULE**

By applying two methods of estimating population size and by including the entire contact sample—both juveniles and adults—a minimum synchronic population size estimate has been calculated for Santa Catalina de Guaule. Because preadults are likely under-represented in the sample, the synchronic population size estimates must be considered a minimum value.

The first estimate of population size for Santa Catalina is derived from the method described by Ubelaker (1984: 96). Population size is measured by the formula:

\[
P = \frac{1000(N)}{MT}
\]

where \(P\) = population size; \(N\) = number of deaths represented by number of individuals recovered; \(M\) = crude mortality rate (number of deaths per 1000 individuals per year); and \(T\) = number of years the cemetery was in use.

For the Santa Catalina de Guaule sample, the minimum number of individuals recovered from the cemetery \((N)\) is 431. The crude mortality rate \((M)\) is represented as a product of \(1/e_x\) \((e_x = \text{life expectancy at birth})\), calculated from data provided in table 3-4 [see Ubelaker, 1984, for formula] and 1000. Crude mortality \((M)\), therefore, is 47.24 years. Finally, we estimate that the cemetery was used for 73 years (1607–1680) (see Larsen, this volume). Therefore, population size \((P)\) is estimated at 125 individuals.

The second method of population size estimation that we applied is that derived by Acsádi and Neméskéri (1970):

\[
P = K + \frac{(D)(e_x)}{T}
\]

where \(P\) = population size; \(K\) = constant \((10\% \text{ of } T)\); \(D\) = number of individuals represented in the cemetery; \(e_x\) = life expectancy at birth; and \(T\) = number of years the cemetery was used. By this formula, population size at Santa Catalina is 132 individuals.

In sum, the minimum synchronic population size estimate for Santa Catalina is 125 to 132 individuals. Swanton (1946) noted that in 1670, the English had observed some 300
men in the mission on St. Catherines Island. Ethnohistoric accounts such as this may tend to overestimate population size for the Guale coast, however. Other scattered census data available from the late 17th century indicate very small populations for towns in the region (G. Jones, 1978).

As pointed out above, given the underrepresentation of juveniles, especially infants, in the Santa Catalina series, it is almost certain that the population estimates presented above are extremely conservative. Comparison with other contact period skeletal samples illustrates this point. For example, in a contact period Arikara skeletal sample from South Dakota, Owseley and Bass (1979) found that 71 percent of the individuals they recovered (N = 652) were less than 20 years of age. In the Santa Catalina de Guale sample, only 41 percent of the individuals recovered were less than 20 years old.

Other confounding problems in a demographic analysis involving mission period human remains is the degree to which mobility of population might influence vital statistics and demographic profiles. It is known that the latter part of the contact period, especially the second half of the 17th century, represents a time of continuous movement of population in this much disputed territory. It is quite possible that part of the Santa Catalina population is buried elsewhere.

Until we have evidence to the contrary, we must assume that the mission cemetery within the church is representative of the individuals and population living in and around Santa Catalina. Undoubtedly, continuing excavation of noncemetery contexts at Santa Catalina as well as study of written documentation for the time period will help elucidate settlement pattern and population size from the archaeological record.

CONCLUSIONS

The results from this study of the precontact preagricultural, precontact agricultural, and contact Georgia coastal demographic profiles suggest that the contact population had longer survivorship than the precontact agricultural community, but was not as robust as the precontact preagricultural population.

A single explanation cannot be posited for these results. It is plausible that there may have been some rebound in overall population health and demographic robusticity during the contact period compared to the preagricultural period. Alternatively, a reduction in growth (reduced fertility and birthrate) may have contributed to higher age-at-death during the contact period in the context of a closed population. It can be argued that estimation of health through demographic means may be best represented by levels of fertility. If reduction in fertility did occur in the contact period—for whatever reason—then we may in fact be looking at a population undergoing decline. However, the incompleteness of at least some of the age cohorts in all three subsamples suggests that paleodemography is not a strong enough tool to stand on its own in explaining the demographic implications of European contact with the Guale. By utilizing the resources of other independent indicators of lifeway and health in the Santa Catalina de Guale sample (see other chapters in this volume), a clearer picture of the impact of changing lifeways associated with European intervention is emerging.

ACKNOWLEDGMENTS

This research was supported by the St. Catherines Island Foundation and the National Science Foundation (award BNS-840773). The figures were prepared by Ms. Lisa L. Gosciejew, Ms. Prisca Kolkowski, and Mr. Barry Stark.
CHAPTER 4. STRESS AND LIFEWAY CHANGE: THE EVIDENCE FROM ENAMEL HYPOPLASIAS

DALE L. HUTCHINSON AND CLARK SPENCER LARSEN

ABSTRACT

Analysis of human remains from the Georgia coast has revealed decline of health in the transition from hunting and gathering to agriculture. Additional stressors present during the contact period in this region—namely, European-introduced diseases, increased emphasis on maize agriculture, warfare, and famine—undoubtedly contributed to an overall decline of native populations.

This study focuses on physiological stress in these populations by examination of dental growth arrest markers known as hypoplasias. For purposes of analysis, the sample has been divided into three periods: precontact preagricultural, precontact agricultural, and contact. Comparisons are made for percent of individuals affected and width of hypoplasias.

In general, there is an increase in percent of individuals affected by enamel hypoplasia in the contact period Santa Catalina de Guale population relative to the precontact agricultural population. Moreover, there is an increase in widths of hypoplastic events over time with the greatest widths in the contact period. These findings suggest either an increase of duration of stress, or an increase in severity of stress events, or a combination of both. Although the contact period Santa Catalina dental series exhibited the greatest widths of hypoplasias, the amount of increase is larger in the preagricultural to agricultural transition than in the agricultural to contact transition. Therefore, the greatest increase in stress may have occurred prior to contact by Europeans in this region.

INTRODUCTION

Assessment of metabolic stress provides an important measure of the relative health of populations. In this sense, stress has been defined by Huss-Ashmore and co-workers as "the physiological disruption of normal metabolic activity of an organism resulting from environmental perturbation" (1982: 396). It is a product of three factors: environmental constraints, cultural systems, and host resistance (Goodman et al., 1984). The degree of stress experienced is related both to the severity of environmental stressors and the degree of host resistance (Huss-Ashmore et al., 1982).

In the present investigation, we utilize an indicator of growth disruption known as enamel hypoplasia. Enamel hypoplasia is a deficiency in enamel thickness on the tooth crown and is manifested by pitting, linear furrowing, or in extreme cases, total lack of enamel (Sarnat and Schour, 1941: Bhaskar, 1986; Suckling et al., 1986; see fig. 4-1). Given the changing profiles of nutrition and disease throughout the record of prehistory and into the contact period on the Georgia coast, this region represents an ideal focus of study dealing with indicators of stress in human populations (see Larsen, this volume).

BACKGROUND AND PREVIOUS RESEARCH

Several skeletal indicators of general episodic stress have been utilized by various researchers. These indicators include growth velocity of long bones (D. Cook, 1984; Goodman et al., 1984; Himes et al., 1975; Garn, 1970; Hummert, 1983), stature decrease (Larsen, 1982), Harris (transverse) lines (Garn et al., 1968; Goodman and Clark, 1981; Maat, 1984), and enamel defects (e.g., Wilson lines, Retzius striae, enamel hypoplasia, and enamel hypocalcification) (references cited below).

Study of Harris lines and enamel defects are important in that their respective occurrence in bones and teeth can be traced to specific years in the growing and developing individual. However, because at least some Harris lines are known to be lost through normal bone remodeling episodes, they are not a desirable stress indicator in past human populations except in a very general sense (Goodman et al., 1984; Hummert and Van Gerven, 1985; McHenry and Schulz, 1976). Enamel, on the other hand, does not remodel and it is subject to changes occurring only within the lifetime of the individual. Therefore, hy-
tentially reveal differences about susceptibility to enamel defect formation across dental polar fields. It has been suggested by a number of workers that polar teeth are the most developmentally stable and under the greatest genetic control (see Butler, 1939; Dahlberg, 1945; Lombardi, 1978). The polar teeth include the maxillary central incisors, mandibular lateral incisors, canines, third premolars, and first molars.

Goodman and Armelagos (1985a) found that within the tooth row anterior teeth are frequently more hypoplastic than posterior teeth. Similarly, they indicate that the more developmentally stable polar teeth exhibit more hypoplasias than nonpolar teeth. In a follow-up study of maxillary incisors and mandibular canines, Goodman and Armelagos (1985b) found that the pattern of defects is similar for location on the tooth crown but dissimilar with regard to age of occurrence. Moreover, "... there is a low frequency of defects in the incisal third and gingival sixth of the crown, and a high frequency in the remaining half of the crown" (Goodman and Armelagos, 1985b: 505).

Several studies indicate that both macroscopic and microscopic enamel defects provide information about nutrition and disease stress (cf. Rose et al., 1985). Attempts to correlate the two types of defects have been less than successful, however. Rose (1977) documented differences between the peak ages of Wilson bands (1.5–3.5 years) and enamel hypoplasias (3.0–3.5 years) for mandibular canines from the Dickson Mounds skeletal
series. Jacobi and Corruccini (1987) examined teeth from a Caribbean slave population and found that enamel hypoplasias which were deeper, wider, and associated with subsurface anomalies (major growth arrests) had a later peak of occurrence than other hypoplasias. Rose and co-workers (1985; citing Condon, 1981) suggested that Wilson bands represent shorter (1–5 day) periods of stress than enamel hypoplasias (weeks to months).

Hypoplasia results from a disturbance in the first stage of matrix deposition (Bhaskar, 1986). Because enamel is deposited in consecutive layers form the occlusal surface to the cervical region of a tooth, some researchers have argued that width of hypoplasias provides a reasonable quantification of duration of a stress event or series of events (Sarnat and Schour, 1941; Blakey and Armelagos, 1985; Walker, in press; Hutchinson and Larsen, 1988). Suckling and co-workers (1986) have demonstrated, however, that severity of stress events plays a vital role in the extent and width of hypoplastic lesions. They noted that

... a range of hypoplastic defects was produced in which the amount of missing enamel was related to the severity of the systemic reaction. ... With insults of increasing severity, fewer ameloblasts retained the capacity for complete or partial recovery of their normal activities. Thus, in sheep, hypoplastic lesions follow damage to the secretory cells by an insult of short duration, the extent and appearance of the affected enamel being determined by the severity of the insult (1986: 432).

A variety of clinical associations have been made between hypoplastic defects and nutritional disorders or disease or both, ranging from metabolic disturbances (e.g., gastrointestinal disorders) to infectious diseases (e.g., syphilis, tuberculosis) (see Cutress and Suckling, 1982; Goodman et al., 1984; Goodman et al., 1987; Hillson, 1986; Hutchinson, 1986; Pindborg, 1970, 1982; Rose et al., 1985). In laboratory animals, hypoplasias have been induced by fever (Kreshover and Clough, 1953b), alloxan diabetes (Kreshover and Clough, 1953a), and tuberculosis (Kreshover, 1944), among other pathogens. Nikiforuk and Fraser (1981; see also Pindborg, 1970) suggested that enamel hypoplasia in deciduous incisors resulted from hypocalcemia caused by chronic diarrhea. Suckling and co-workers (1983) demonstrated similar results for sheep with induced parasitism. They found that acute diarrhea was associated with more severe forms of hypoplasia. Skinner and Hung (1989) have suggested that minor localized trauma may cause enamel defects.

Attempts in clinical situations to correlate specific diseases and hypoplasia in a causal relationship have generally not been successful (Massler et al., 1941). Consequently, most researchers follow the conservative steps of Kreshover (1960) in recognizing that hypoplasia is a nonspecific indicator of metabolic stress usually resulting from nutritional deficiencies or infectious disease or a combination of the two (see also Suckling et al., 1986). In archaeological series, there have been attempts to relate specific diseases with hypoplasia occurrences (e.g., Knick, 1981), but until a clearer understanding of the etiology of disease and its impact on the developing dentition is made, conclusions should be considered tentative in this regard.

MATERIALS AND METHODS

The Santa Catalina de Guale population is represented by 229 dentitions in this study. In addition, teeth representing 141 individuals from precontact preagricultural Georgia coastal mortuary localities dating before A.D. 1150, and 140 individuals from the precontact agricultural Irene Mound site (A.D. 1150–1450) were also selected for analysis (table 4-1).

Prior to study, all tooth surfaces were cleaned with acetone to remove debris. Following cleaning, the labial surface of each tooth was examined at the midsagittal plane by use of a stereozoom, binocular microscope at a fixed power of approximately 10×. The superior and inferior margins of hypoplasias were measured relative to the cementoenamel junction of each tooth using a micrometer mounted on the eyepiece of the microscope and set at 0.1 mm increments at the level of tooth observation. It is our experience that the use of a microscope greatly facilitated the location of enamel defects and provided a more consistent means of measurement than with use of calipers. Figure 4-2 shows a hypoplastic canine at the approximate magnification used in measurement.

Many dentitions exhibited some degree of
TABLE 4-1
Dentitions from Georgia Coastal Mortuary Sites

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<tr>
<th>Site</th>
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<th>Reference</th>
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</tr>
<tr>
<td>Cunningham Mound C</td>
<td>2</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Cunningham Mound D</td>
<td>2</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Cunningham Mound E</td>
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<td>McLeod Mound</td>
<td>11</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Seaside Mound I</td>
<td>8</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
<td>Seaside Mound II</td>
<td>5</td>
<td>Thomas and Larsen, 1979</td>
</tr>
<tr>
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<td>2</td>
<td>Larsen and Thomas, 1982</td>
</tr>
<tr>
<td>Johns Mound</td>
<td>28</td>
<td>Larsen and Thomas, 1982</td>
</tr>
<tr>
<td>Airport Site</td>
<td>19</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Deptford Site</td>
<td>10</td>
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</tr>
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<td>Cannons Point</td>
<td>6</td>
<td>Larsen, 1982</td>
</tr>
<tr>
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<td>17</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>Charlie King Mound</td>
<td>17</td>
<td>Larsen, 1982</td>
</tr>
<tr>
<td>South End Mound I</td>
<td>1</td>
<td>Larsen and Thomas, 1986</td>
</tr>
<tr>
<td>South End Mound II</td>
<td>12</td>
<td>Larsen and Thomas, 1986</td>
</tr>
<tr>
<td>Precontact agricultural</td>
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<td></td>
</tr>
<tr>
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<td>Caldwell and McCann, 1941</td>
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<td></td>
</tr>
<tr>
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<td>229</td>
<td>Larsen, this volume</td>
</tr>
</tbody>
</table>

occlusal attrition which might obliterate hypoplastic events, thereby potentially lending a bias to results. One approach to eliminate bias which might result from differential degrees of attrition has been to report the ratio of cases examined to those exhibiting hypoplastic defects for each age category (cf. Powell, 1988; Walker, in press). Goodman and Armelagos (1985a) reported that most hypoplasias occur in the middle and cervical thirds of teeth (see also Condon, 1981). Only one-fifth or fewer occur on the occlusal third of tooth crowns on the teeth studied from Santa Catalina and other Georgia coastal populations discussed here. Therefore, it is unlikely that dental attrition would account for the differences observed between samples (see below).

Hypoplasias on eight permanent teeth were recorded and analyzed—the mandibular and maxillary central and lateral incisors (I1, I2), canines (C), and first molars (M1) (table 4-2). Ages were determined for hypoplastic events within half-year intervals utilizing the developmental chronology developed by Maslcer and co-workers (1941), and modified for use by Swärdstedt (1966) and Goodman et al. (1980). Hutchinson (1986; Hutchinson and Larsen, 1988) has presented a more detailed discussion of methodology elsewhere.

In order to avoid duplication of hypoplastic events through the use of paired teeth, teeth from the left side of the dentitions were examined. In the case of a missing tooth, the right tooth was substituted if available. Results in this study are reported by individual tooth types because of differential susceptibility and timing of hypoplastic defects between different tooth types (cf. Goodman and Armelagos, 1985a, 1985b).

Two measures of hypoplastic enamel were obtained for this study. The first measure includes area which is the sum total of widths of hypoplastic enamel within each half-year age interval. This measure, therefore, can involve either one or more hypoplasias in that it represents a sum of individual hypoplastic episodes within a half-year. The second measure includes event which consists of the total continuous width of a single hypoplastic occurrence regardless of age boundary (fig. 4-1).

RESULTS

All tooth types, except the first molars, demonstrate that a higher percentage of pre-
FIG. 4-2. Labial surface of permanent right mandibular canine. Note the presence of a groove and adjacent line of pits located within a continuous zone of hypoplastic activity extending from the mid-crown to the cementoenamel junction (approximately 10×).

Contact preagricultural individuals experienced at least one episode of growth arrest when compared with individuals interred at Santa Catalina (fig. 4-3). Statistically significant differences ($p < 0.05$; chi-square) in the number of individuals affected were found for the mandibular lateral incisor and first molar, and the maxillary lateral incisor.

The number of individuals affected by at least one hypoplasia during the contact period is more similar to the precontact agricultural period than to the precontact preagricultural period (fig. 4-3). For all tooth types, except the mandibular lateral incisor, more individuals were affected in the contact period Santa Catalina sample than in the precontact agricultural period. This difference is statistically significant ($p < 0.01$: chi-square) for the mandibular first molar and the maxillary first molar.

Comparison of mean area, the total amount (width) of enamel affected by hypoplasia within half-year age intervals, shows that for all tooth categories, except the mandibular central incisor, the contact individuals experienced more stress than the precontact preagricultural individuals (fig. 4-4). Significant differences were indicated for the maxillary central incisor ($p < 0.05$: Student’s $t$-test), and for the mandibular and maxillary canines ($p < 0.01$: Student’s $t$-test).

The contact Santa Catalina and precontact agricultural comparison of mean area shows much the same relationship (fig. 4-5). For the mandibular canine and first molar, and the maxillary lateral incisor, maxillary, and first molar, the contact period teeth have a higher mean. Hypoplastic area is significantly different for the mandibular central incisor between the two populations ($p < 0.05$: Student’s $t$-test).

Comparison of mean hypoplasia events of the contact and precontact preagricultural populations as measured by single continuous hypoplastic bands shows significantly higher means for all teeth from the contact mission population except the mandibular central incisor (fig. 4-6). This difference is statistically significant ($p < 0.01$: Student’s $t$-test) for the mandibular canine and the maxillary lateral incisor and canine. However, with the exception of the mandibular lateral incisor, all tooth categories had a greater mean for the contact population.

<table>
<thead>
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<th>Contact</th>
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<td></td>
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<td>agricultural</td>
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</tr>
<tr>
<td>Mandibular</td>
<td>(N)</td>
<td>(N)</td>
<td>(N)</td>
</tr>
<tr>
<td>I1</td>
<td>40</td>
<td>65</td>
<td>84</td>
</tr>
<tr>
<td>I2</td>
<td>57</td>
<td>77</td>
<td>90</td>
</tr>
<tr>
<td>C</td>
<td>79</td>
<td>97</td>
<td>138</td>
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<tr>
<td>M1</td>
<td>64</td>
<td>61</td>
<td>102</td>
</tr>
<tr>
<td>Maxillary</td>
<td>(N)</td>
<td>(N)</td>
<td>(N)</td>
</tr>
<tr>
<td>I1</td>
<td>53</td>
<td>65</td>
<td>77</td>
</tr>
<tr>
<td>I2</td>
<td>49</td>
<td>66</td>
<td>77</td>
</tr>
<tr>
<td>C</td>
<td>67</td>
<td>81</td>
<td>128</td>
</tr>
<tr>
<td>M1</td>
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<tr>
<td>Total</td>
<td>471</td>
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</table>
The mean of hypoplasia events for the precontact agricultural Irene Mound population compared to the contact population is displayed in figure 4-7. In half of the tooth categories, precontact agricultural individuals experienced stress events that were wider than contact individuals. These differences between the two populations were significant ($p < 0.05$: Student’s $t$-test) for the mandibular central incisor and maxillary canine. When considering the frequencies of continuous hypoplasias, however, precontact agricultural individuals experienced fewer hypoplasias for all tooth types except the mandibular canine and lateral incisor (see fig. 4-12).

The age at which growth arrest occurs is an important variable in attempting to delineate the conditions under which stress occurred. For the present study, therefore, we have chosen two measures of the relative ages of enamel defect formation for the mandibular canine and maxillary central incisor: (1) frequency of enamel defects by age category; and (2) enamel defect area by age category (cf. Goodman and Armelagos, 1985b).

Frequency of defects here follows the approach defined by Blakey (1981): hypoplasias which occur across age interval boundaries are counted as one event per age interval of their occurrence. Frequency, in this sense,
HYPOPLASIA AREA

![HYPOPLASIA AREA](image)

Fig. 4-4. Comparison of precontact preagricultural and contact hypoplasia area (mean of widths within half-year age intervals).

measures the sum of partial or whole enamel hypoplasias or both in each age interval. On the other hand, the sum of the widths of these hypoplasias bounded by age increments is the area of hypoplasia activity.

The percentage of total hypoplasia area contributed by each half-year period for the maxillary central incisor is shown in figure 4-8. The peak of hypoplasia activity occurs at ages 2.5 to 3.5 years. Mean area for the same tooth shows a similar pattern (fig. 4-9).

Mean frequency of defects for the mandibular canine shows that a peak of hypoplasia activity occurs later, between the ages of 3.5 to 4.5 years (fig. 4-10). Mean area shows a similar pattern (fig. 4-11).

Comparison of the mean frequency and mean width of continuous enamel hypoplasias for each tooth type for the precontact and contact samples is presented in figure 4-12.

With regard to dental field analysis, we are unable to address the issue of susceptibility of the first molars relative to other teeth in their dental field because other teeth in that particular dental field were not examined. In agreement with the results of other workers (e.g., Goodman and Armelagos, 1985a, 1985b), Georgia coastal anterior teeth are clearly more hypoplastic than the posterior teeth (fig. 4-3). As expected, when considering mean frequency of enamel defects, the mandibular lateral incisors appear to be relatively more susceptible to hypoplasia than central incisors. With the exception of the precontact preagricultural group, maxillary incisor defect patterning exhibits the expected pattern of increased susceptibility for the central incisor.

The field theory, however, explains less with regard to differences in widths of continuous
HYPOPLASIA AREA

Fig. 4-5. Comparison of precontact agricultural and contact hypoplasia area (mean of widths within half-year age intervals).

DISCUSSION

Previous studies based on populations worldwide have shown that the transition from a hunting-gathering lifeway to one based on agriculture is associated with a decrease in general health (Cohen and Armelagos, 1984; Larsen, 1982, 1984). With this transition on the Georgia coast, the addition of maize agriculture to the subsistence economy likely reduced resource diversity and dietary quality (see Larsen, 1982, 1984, this volume; Schoeninger et al., this volume). Maize is a rather poor source of protein, and populations dependent on maize exhibit a general decline in dental health, particularly as revealed by an increase in cariogenic activity and deficient enamel development (cf. Cohen and Armelagos, 1984).

In general, malnutrition and infectious disease are characterized by a synergistic relationship. Poor nutrition, especially protein deficiency, will lower an individual's resistance to infection and depress the cell-mediated immune response (Hoffman-Goetz, 1986; Mims, 1982). Infectious disease inter-
Fig. 4-6. Comparison of precontact preagricultural and contact hypoplasia events (mean of widths for hypoplasia event regardless of age).

...fers with nutrition by altering absorption in the digestive system and increasing the physiological needs for nutrients, especially protein. Consequently, when an organism is placed under stress, it will either slow or cease growth while nutrients are oriented to combat stress (Acheson, 1960).

Studies utilizing enamel hypoplasia as a stress indicator have generally demonstrated an increase in frequency or widths of defects in the transition from hunting and gathering to agriculture (see various studies in Cohen and Armelagos, 1984; but see Hodges, 1987). At Dickson Mounds, for example, Goodman et al. (1984) reported an increase in hypoplasias from 45 percent for the Late Woodland to 80 percent for the Mississippian populations. Similarly, Perzigian and co-workers (1984) reported that the Mississippian Fort Ancient teeth have three times as many hypoplasias as the earlier Middle Woodland or Archaic Ohio groups.

With the arrival of Europeans in Spanish Florida and subsequent establishment of mission centers, further emphasis was placed on agriculture not only for maintenance of Native Americans and Europeans at these centers, but for St. Augustine to the south as well. These problems were probably compounded by other stressors (Larsen, this volume; Crook, 1986). In particular, the introduction of Old World infectious diseases, forced labor, demands of food tribute, harassment by local military, and retaliation for native revolts resulted in destruction of crops and stored foods (cf. Jones, 1978; Dobyns,
Fig. 4-7. Comparison of precontact agricultural and contact hypoplasia events (mean of width for hypoplasia event regardless of age).

1983; Milner, 1980; Loucks, 1979; Bushnell, 1987).

The mission effort in the region also resulted in a greater nucleation of local populations into a few population centers associated with the missions. The spread of infectious diseases, both of New World and Old World derivation, was undoubtedly enhanced by these settlement changes.

Comparison of precontact preagricultural, precontact agricultural, and contact period populations from the Georgia coast shows a general increase in the width of continuous hypoplasias. The greater width of hypoplastic defects could be indicative of either severity or duration or perhaps both. Recent developments in counting incremental growth markings of teeth (e.g., Dean, 1987; Beynon and Dean, 1988) have added greater precision to timing of tooth growth. By counting these markings (e.g., Retzius striae) in hypoplastic teeth, it may be possible to determine by independent means the time involved in producing a hypoplastic event or series of events (Condon, personal commun.).

Teeth that appear to be more susceptible to physiological stress—incisors and canines—show an increase in frequency of defects. It is not entirely clear to us why there is an increase in defects in these teeth. Perhaps of greater importance, however, is the finding that the teeth that seem to be least susceptible to hypoplasia—the molars—have the highest number of defects in the contact period Santa Catalina population relative to the precontact populations. Goodman and
Fig. 4-8. Comparison of precontact preagricultural, precontact agricultural, and contact frequency (in percent) of total hypoplasia area by age for maxillary central incisor.

Armelagos (1985a) suggested that the presence of hypoplasias on less susceptible teeth may reflect relatively greater severity of stress. Certainly given the extreme environmental conditions that these populations experienced, the greater frequency of enamel defects in contact period molars compared to precontact period molars may indeed reflect greater stress loads in these later populations.

The decline in percentage of individuals affected by growth arrests for the Santa Catalina population with concomitant increase in stress hypoplasia width suggests that stress may have become more acute. In this regard, Goodman and co-workers (1980) compared populations from Illinois sites and demonstrated that the hunter-gatherer population exhibited signs of seasonal stress as manifested by enamel hypoplasia. This chronic form of stress may have had its primary effect on morbidity. Mortality, on the other hand, may have been more affected by a later combination of stressors, particularly those present during the contact period and not before.

Comparison of the contact period Santa Catalina and precontact agricultural Irene Mound populations reveals a relatively greater similarity in pattern of hypoplasia events, frequency of continuous hypoplasias, and percentage of individuals affected than comparison of the Santa Catalina and precontact preagricultural populations. One possible bias that may have influenced these findings is the less homogeneous precontact preagricultural sample. That is, both the contact and the precontact agricultural populations are represented by dentitions from single sites of relatively short periods of cemetery use (Santa
LARSEN: SANTA CATALINA DE GUALE. 2

Fig. 4-9. Comparison of precontact preagricultural, precontact agricultural, and contact mean hypoplasia area by age for maxillary central incisor.

Catalina = 73 years; Irene Mound = ca. 300 years. In contrast, the precontact preagricultural sample comprises individuals from a number of sites spanning a relatively long period of cemetery use (ca. 1500 years). Larsen (1982) has suggested, however, that archaeological evidence indicates general uniformity of subsistence in the precontact preagricultural period (see also discussion in Schoeninger et al., this volume).

We have argued that those individuals from the Santa Catalina population who experience stress earlier in life are predisposed to increased morbidity and mortality (Simpson et al., 1986, this volume). If increased mortality played a major role in the aboriginal contact experience, then those individuals who experienced acute stress due to epidemic disease might not develop morbid indicators of that stress (e.g., hypoplasias).

The studies on contact period mission populations are too sparse to provide a basis for broad comparisons in this regard. Storey (1986) has compared precontact and contact period dental remains from the Florida panhandle and found that the later dentitions showed a reduction in frequency of enamel defects. Walker (in press) compared historic mission and prehistoric populations from the Santa Barbara Channel area of southern Cal-
California. In contrast to the findings from the Georgia coast, this investigator reported narrower hypoplasias in the mission sample compared to the earlier precontact sample. He suggested that there was a reduction in duration of stress in the contact period relative to the precontact period which may reflect superior health care in the later contact period populations. The remains from California are later than those from Santa Catalina and may represent a population that had more time to adjust to novel stressors arising from contact with Old World populations.

It is clear from other studies (e.g., Goodman and Armelagos, 1985a, 1985b) that there is still much to be learned about the detailed nature of differential effects of general metabolic stress on dental hard tissues. Several areas of inquiry require further attention. The occurrence of hypoplasias at specific ages or specific locations on the tooth crown is especially problematical.

With regard to specific ages, Sarnat and Schour (1941, 1942) reported that about two-thirds of hypoplasias in an American urban population occurred in the first year after birth. Only 2% of this population developed hypoplasias after the third year. Subsequently, this age of occurrence was adopted as a standard by the dental profession (Giro, 1947; Massler et al., 1941; Vila, 1949; and see discussion by Goodman [1988]). Examination of archaeological dentitions does not support such an early age of peak hypoplasia occur-
rence, however. The peak occurrence of 2.5–4.5 years demonstrated for the coastal Georgia populations is comparable to that found in other studies of Amerindian samples (see table 4-3).

The peak in hypoplasia occurrence at three to four years has been interpreted most commonly as representing the stress of weaning and a shift to a poor diet (Black, 1979; Clarke, 1980; Corruccini et al., 1985; Goodman et al., 1984). Infant diarrhea quite often occurs in the shift from milk provided by the mother to poor nutrition. The resulting introduction of previously unexperienced pathogens may be influential in causing malnutrition during these critical years of growth and development.

With regard to specific locations on the tooth crown, Black (1979) found no hypoplasias on the apical half of any teeth, not even for individuals whose other teeth were growing in the cervical half at the same time and had hypoplasias. Other researchers report similar findings for the age of occurrence of hypoplasia (e.g., Jacobi and Corruccini, 1987; Rose, 1977). As discussed above, Goodman and Armelagos (1985a, 1985b) have reported that hypoplasias in the Dickson Mounds series occur most frequently in the cervical and middle thirds of the tooth.

Fig. 4-11. Comparison of precontact preagricultural, precontact agricultural, and contact mean hypoplasia area by age for mandibular canine.
Fig. 4-12. Comparison of precontact preagricultural, precontact agricultural, and contact mean frequency and mean width of continuous enamel hypoplasias for each tooth type.

crown, thereby suggesting a region-specific nature of hypoplastic activity in teeth.

An important factor in determining where on the tooth crown hypoplasias occur during growth and development may be related to the way enamel forms. Hillson (1986: 139) noted:

Hypoplasia is usually only visible at the surface of a crown after the formation of the "last dome" of enamel. It is events at the edge of each sleeve of enamel deposited thereafter that are recorded. Thus only a part of each crown will yield information at the surface. Likewise, hypoplasia becomes more prominent towards the slower growing cervical region.

Rate of enamel matrix deposition and crown development may also be of vital importance in determining where on the crown hypoplasias form. Condon (1988), for example, suggested that the middle portion of incisors, canines, and premolars exhibits a slower rate of enamel matrix deposition, thereby increasing susceptibility of hypoplasia formation (but see Goodman and Armelagos, 1985b).

CONCLUSIONS

Measurement of stress utilizing only the presence or absence of enamel hypoplasia does not take into consideration other data. We have demonstrated that the measurement of the quantity of growth disturbances in Georgia coastal dentitions provides a more precise measure of stress and the nature of change in episodes of stress events.

The precontact preagricultural population experienced more single stress events than either the Irene Mound or Santa Catalina populations, but the mean width of hypoplasias was narrower. Similarly, more precontact preagricultural individuals were affected than either of the other two groups. Although
TABLE 4-3
Comparative Ages of Hypoplasia Occurrence

<table>
<thead>
<tr>
<th>Source</th>
<th>Period</th>
<th>Age range</th>
<th>Age peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>Berryman, 1981</td>
<td>Mississippian</td>
<td>0.0–12.5</td>
<td>0.5–5.5</td>
</tr>
<tr>
<td>Corruccini et al., 1985</td>
<td>Historic</td>
<td>0.0–6.5</td>
<td>3.0–4.0</td>
</tr>
<tr>
<td>Goodman et al., 1980</td>
<td>LW/MALWa</td>
<td>0.0–6.0</td>
<td>3.0–3.5</td>
</tr>
<tr>
<td>McManammon et al., 1986</td>
<td>Mississippian</td>
<td>0.0–5.5</td>
<td>2.5–3.0</td>
</tr>
<tr>
<td>Powell, 1988</td>
<td>Late Woodland</td>
<td>0.0–6.0</td>
<td>2.5–5.5</td>
</tr>
<tr>
<td>Rose et al., 1978</td>
<td>Mississippian</td>
<td>1.5–6.0</td>
<td>2.5–4.5</td>
</tr>
<tr>
<td></td>
<td>Middle Woodland</td>
<td>0.5–4.0</td>
<td>even</td>
</tr>
<tr>
<td></td>
<td>MALWb</td>
<td>2.0–4.5</td>
<td>2.0–2.5</td>
</tr>
<tr>
<td></td>
<td>Mississippian</td>
<td>1.0–3.5</td>
<td>1.75, 3.25</td>
</tr>
<tr>
<td>Schüttler and McHenry, 1975</td>
<td>Prehistoric</td>
<td>1.0–7.0</td>
<td>4.0–5.0</td>
</tr>
<tr>
<td>Swärdstedt, 1966</td>
<td>Medieval</td>
<td>—</td>
<td>2.0–4.0</td>
</tr>
<tr>
<td>Walker, in press</td>
<td>Prehistoric</td>
<td>1.0–6.5</td>
<td>2.0–5.0</td>
</tr>
<tr>
<td></td>
<td>Contact</td>
<td>2.5–6.0</td>
<td>3.0–5.0</td>
</tr>
</tbody>
</table>

*a Late Woodland/Mississippian Acculturated Late Woodland.  
*b Mississippian Acculturated Late Woodland.

we do not fully understand the causal factors involved in the decline in lifeway discussed here, one thing is certain: the precontact agricultural and contact periods are more similar to each other in levels of metabolic stress than either is to the precontact preagricultural period. Moreover, analysis of these data suggest that the transition from a lifeway based on hunting and gathering to one based at least in part on maize agriculture occasioned relatively greater increase in metabolic stress than did the transition in lifeway associated with the arrival of Europeans and the establishment of mission centers. These conclusions are especially clear cut in comparison of mean of events of hypoplastic activity between the three periods. We suggest that the greater widths of individual hypoplasias in the precontact agricultural and contact populations represent either an increase in severity or duration of stress or both.

We should provide the caution, however, that this study reports on one stress indicator. Future research will focus, in part, on utilizing this approach in concert with other avenues of investigation. Incorporation of other lines of evidence, both biological and non-biological, will probably be needed in order to delineate further those changes in health and lifeway that pertain specifically to either the precontact agricultural or contact lifeway transitions.

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The figure artwork was prepared by Ms. Lisa L. Gosciejew and Ms. Prisca Kolkowski.
CHAPTER 5. COPING WITH STRESS: TOOTH SIZE, DENTAL DEFECTS, AND AGE-AT-DEATH

SCOTT W. SIMPSON, DALE L. HUTCHINSON, AND CLARK SPENCER LARSEN

ABSTRACT

This study examines the relationship between age-at-death and dental stress indicators by analysis of tooth size and frequency, width, and timing of hypoplasias. Within populations, there is a differential ability to mitigate the effects of extrinsic stressors. Individuals that are less able to reduce the effects of the external stress environment (e.g., infectious disease and nutritional deprivation) should exhibit higher morbidity and increased frequency of developmental defects. Therefore, younger individuals in a stressed setting should exhibit a greater frequency or severity of developmental anomalies—including smaller teeth and greater hypoplastic activity—than older individuals. This may involve a different temporal pattern of stress events in individuals who died at an earlier age relative to individuals who survived longer.

This hypothesis was tested by examination of the Santa Catalina de Guale dental material. Comparisons were made for tooth size (breadth) and enamel hypoplasias (frequency, location, and width) in two mortality cohorts: preadults (less than 18 years) and adults (18 years and older).

The analysis of data demonstrates that the preadult cohort has smaller tooth crowns than the adult cohort. However, no clear differences were found in frequency of hypoplastic activity, timing of metabolic disruption, or width of hypoplasias between the preadult and adult cohorts. These findings suggest that individuals stressed earlier in life were more predisposed to subsequent stress, thus reducing their ability to survive into later life.

INTRODUCTION

Differential survivorship in human populations is a result of many causes relating to environment, diet, society, and constitution. It is one of the elements of evolution through which we can examine and interpret the ways that humans adapt to their environment through biosocial processes. In a complex environment, there will be a differential or non-random ability of individuals within a population to mitigate ambient stressors. Individuals who are not able to reduce the effects of stressors should exhibit generally higher morbidity and mortality. Individuals in a population who die at younger ages tend to be those who are less capable of reducing the effects of stressors. Individuals who die at earlier ages, therefore, should exhibit a greater frequency and severity of stress indicators.

As a follow-up to the previous chapter (Hutchinson and Larsen), we examine the juxtaposition of two factors, age-at-death and the presence of dental stress indicators. An inverse relationship between age-at-death and the presence, frequency, and severity of stress indicators in teeth is hypothesized. This hypothesis was tested by a comparison of the stress indicator profiles of preadult and adult death cohorts representing the contact period Santa Catalina de Guale skeletal series from the Georgia coast.

TEETH AS AN INDICATOR OF STRESS

The use of teeth as a physiological indicator of stress has been widely applied on the microscopic level to examine deviances in the enamel microstructure, such as Wilson bands and striae of Retzius (Molnar and Ward, 1975; Rose et al., 1978), and on the macroscopic level for enamel hypoplasias (Rose, 1977, 1979; Sciulli, 1978; Goodman et al., 1980, 1984; Huss-Ashmore et al., 1982; Larsen, 1987; Hutchinson and Larsen, 1988, this volume), circular caries (Cook and Buikstra, 1979), fluctuating dental asymmetry (Doyle and Johnson, 1977; O'Connell, 1983), and tooth size (Garn et al., 1979; Guagliardo, 1982).

Tooth size has been shown to have a significant nongenetic, environmental compo-
nent. Townsend and Brown (1978), for example, estimated that up to 36 percent of the total variance in tooth crown size is due to environmental factors. Although other estimates vary widely in this regard (see, for example, Corruccini and Potter, 1981; Potter et al., 1968, 1976; Osborne et al., 1958; Alvesalo and Tigerstedt, 1974; Goose, 1971; Goodman, 1965), the consensus has developed that environment can potentially influence tooth crown size. The period of growth and development of tooth crowns (four months in utero to 12 years) corresponds with a time of greater stress in most human populations (Gordon et al., 1963). Therefore, in the absence of gene flow or selection, tooth size differences may reflect the degree of variance resulting from extrinsic (environmental) factors during the period of tooth development.

Tooth size reduction and developmental anomalies due to external disturbances or increased stress loads have been documented in living populations (Evans, 1944; Bailey et al., 1968; Goose, 1971; Garn et al., 1979, 1980). However, differences in tooth size resulting from differential stress have only recently been used in biocultural reconstructions of past populations (e.g., Guagliardo, 1982; Larsen, 1982, 1983c).

Enamel hypoplasia is a deficiency in enamel development that results from disruption of ameloblastic apposition. Tooth size has received only minor recognition as an indicator of stress (e.g., Guagliardo, 1982), but the use of enamel hypoplasias as well as other enamel developmental defects has had a longer and more prolific history in both clinical and anthropological settings (Massler et al., 1941; Schour and Massler, 1945; Swärdstedt, 1966; Schulz and McHenry, 1975; McHenry and Schulz, 1976; Goodman et al., 1980; Goodman and Armelagos, 1985a, 1985b; and others).

Tooth size and enamel hypoplasia were selected for this study because of their analogous response in the face of metabolic disruption. Tooth size provides a rough measure of deviation from the genetic growth potential and enamel hypoplasias can provide documentation for the timing and possibly extent of growth disruption. Thus, factors influencing absolute tooth crown size and formation of enamel hypoplasias have different, yet overlapping, temporal windows of development.

Tissue maturation is best interpreted as a complex combination of developmental and growth processes. The tenor of tissue development is influenced by both genetic and environmental factors. The critical denominator during the growth process is the availability of an adequate nutrient supply. Malnutrition during gestation has been demonstrated to result in a number of problems in offspring at both the cellular and the tissue levels (Minckler et al., 1971). These problems include low birth weight, shorter neonates, elevated morbidity and mortality, reduced growth in general and of the neural and dental tissues in particular (summarized in DePoala and Kufnec, 1976; Frisrancho et al., 1977; Whitney and Hamilton, 1981; Stinson, 1985; Garn et al., 1979).

Growth of cellular structures is dependent on the availability of amino acids, a factor ultimately regulated by diet (DePoala and Kufnec, 1976) and the health status of the individual. Protein synthesis is necessary for normal growth. Fetal growth is more complex because proteins are not transmitted across the placental barrier. Only the protein substrates (amino acids) are passed by the mother to the fetus, and the fetus must then synthesize its own protein. In the absence of this pool of available amino acids, severe developmental problems can result, including retardation of growth (Minckler et al., 1971).

This deficiency may result in decreased metabolic activity, thereby influencing the growth and maturation of the developing structure. The genetic control of a structure is manifested in two broad categories: (1) the timing of the histodifferentiation, and (2) the setting of the minimal and maximal limits of size. Environmental factors modify growth by changes in the timing of enzymatic activity or by limiting the ability of a cell or structure to attain the full genetic potential as a result of a reduction in the availability of the substrates for growth, the amino acids.

Developmental irregularities during the hyperplastic and hypertrophic stages may have different consequences for the final morphology of teeth. Disruption during the hyperplastic (differentiation) stage of dental de-
velopment, such as that caused by vitamin deficiency (Bhaskar, 1986), may result in a number of severe anomalies (e.g., agenesis, irregular morphology, reduced or supernumerary cusps, delayed eruption). Whereas, growth disruptions during the hypertrophic phase would result in alterations in the size of the developing structure.

Alterations of the overall enamel dimensions can also occur during the period of amelogenesis or during the apposition of enamel. A delay in enamel production during calcification or matrix formation could reduce the thickness of the enamel walls, thereby reducing their relative contribution to the final crown dimension. The size of the dental papilla is not altered once amelogenesis commences. Although local attenuation of the enamel crown through ameloblastic slowdown (hypoplastic waisting) is a possible influencing factor for a measured reduction in the breadth of the enamel crown, hypoplastic activity is usually very shallow in depth and rather narrow in breadth. These areas of enamel hypoplasias are generally bounded by adjacent areas of normal enamel indicating that ameloblastic activity was not impaired. What this means for overall tooth dimension is that changes in the enamel crown are generally localized and tend not to contribute to the overall diminution of the tooth.

Although there is a strong relationship between congenital anomalies—for example, Down's syndrome, hypodontia, cleft palate—shown to have a reducing effect on tooth size and age-at-death (Cohen et al., 1977; Townsend et al., 1984), the very low frequencies at which these individuals are present in a normal population probably does not significantly skew the tooth size profile of the preadult cohort. The effects of congenital anomalies are probably not, therefore, a confounding factor in this analysis.

MATERIALS AND METHODS

Dental samples representing 238 individuals from Santa Catalina de Guale were analyzed. Crown breadths (buccal-lingual diameter) were recorded for all individuals in the series and for all permanent teeth, excluding the maxillary and mandibular third molars. Crown length (mesial-distal diameter) is not included here due to its age-related change in size through interproximal attrition (Wolpoff, 1971; Brace et al., 1987). Crown dimensions were measured to the nearest 0.1 mm following procedures described elsewhere (Larsen, 1982).

Of the 238 individuals, 219 (144 adults, 75 preadults) were examined for hypoplasias. Widths and location of hypoplastic defects relative to the cementoenamel junction were recorded on the maxillary and mandibular permanent central incisor (I1), lateral incisor (I2), and canine (C) following procedures outlined by Hutchinson and Larsen (1988, this volume). Hypoplastic events of less than 0.2 mm were not included.

For purposes of analysis, the samples were divided into two age-at-death cohorts, preadult (<18 years) and adult (18+ years). Age was determined following dental development and functional age changes outlined by Russell and co-workers (this volume).

RESULTS

TOOTH SIZE: Table 5-1 and figure 5-1 show the percentage and absolute size differences, respectively, for preadult and adult crown breadths. Comparison of preadult and adult tooth crown breadths reveals a clear pattern of smaller size preadult teeth. Of the 14 tooth types examined, nine of them are smaller in the preadult cohort than the adult cohort. The remaining five tooth types show no difference in size for one tooth and smaller size in adults for the remaining four. All of the statistically significant differences noted (Student's t-test: p < 0.05) are in the direction of smaller size teeth for the preadult group (mandibular canine, third premolar, fourth premolar). Evaluation of the individual distributions of each tooth type for both samples indicates that all of the distributions approximate normality and that their respective shapes are neither skewed nor kurtotic.

An examination of figure 5-1 shows that the mandibular teeth exhibit a greater amount of size difference between the preadult and adult cohorts than the maxillary teeth. Of the three statistically significant differences, none of them are found in the maxillary dentition. These data suggest that the mandibular teeth
may be more developmentally sensitive than the maxillary teeth (see also Guagliardo, 1982; Simpson, 1987).

**ENAMEL HYPOPLASIAS:** The hypoplasia profiles are not greatly different between the preadult and adult age cohorts (table 5-2). Examination of individual tooth types shows a great range in percent difference between preadults and adults. Inspection of these data indicates that fewer adults are affected by hypoplasia than preadults (table 5-2). The difference ranges from 5 percent (maxillary canine) to 12 percent (mandibular central and lateral incisors, and maxillary canine). Only one tooth—the mandibular canine—shows a higher percent in adults than preadults. None of the differences are statistically significant (chi-square: all values of \( p > 0.05 \)). Nevertheless, preadults show a tendency for a greater frequency of hypoplastic individuals than the adults at Santa Catalina, although non-developmental factors (e.g., dental attrition) (see below) may account for this difference.

The pattern of onset of the hypoplasia producing episodes is not significantly different between the preadult and adult cohorts (figs. 5-2, 5-3). Close examination of these data indicates, however, that the preadult group shows, in general, a slightly earlier age of onset. Similar frequencies of hypoplastic episodes are distributed relatively evenly across the age categories although some insignificant variation is present. For example, in the mandibular central incisor and the maxillary canine, hypoplasias are present in two half-year age categories earlier in the preadult group than the adult group. The pattern is reversed for the mandibular lateral incisor. That is, the adult group exhibits a small percentage of hypoplasia area one age class earlier than does the preadult cohort.

The other teeth (mandibular canine, maxillary central and lateral incisors) exhibit little difference in this respect. Overall, the total age-specific patterns of hypoplasia onset for all of the tooth types tend to approximate each other.

The width of hypoplastic bands does not appear to correlate with age-at-death (table 5-3). Three of the tooth comparisons show wider bands in the preadult group (mandibular central incisor, canine, maxillary central incisor), and likewise, three comparisons show wider bands in the adult group (mandibular

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**TABLE 5-1**

**Mean Tooth Breadth Comparisons for the Preadult and the Adult Cohorts from Santa Catalina de Guale**

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Preadult</th>
<th>Adult</th>
<th>Percent difference&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Maxillary</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>(16)</td>
<td>7.66</td>
<td>0.56</td>
</tr>
<tr>
<td>I2</td>
<td>(23)</td>
<td>6.94</td>
<td>0.39</td>
</tr>
<tr>
<td>C</td>
<td>(28)</td>
<td>8.59</td>
<td>0.66</td>
</tr>
<tr>
<td>P3</td>
<td>(34)</td>
<td>10.12</td>
<td>0.59</td>
</tr>
<tr>
<td>P4</td>
<td>(25)</td>
<td>9.77</td>
<td>0.56</td>
</tr>
<tr>
<td>M1</td>
<td>(38)</td>
<td>11.93</td>
<td>0.68</td>
</tr>
<tr>
<td>M2</td>
<td>(21)</td>
<td>12.09</td>
<td>0.67</td>
</tr>
<tr>
<td>Mandibular</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>(20)</td>
<td>5.84</td>
<td>0.38</td>
</tr>
<tr>
<td>I2</td>
<td>(27)</td>
<td>6.23</td>
<td>0.40</td>
</tr>
<tr>
<td>C</td>
<td>(32)</td>
<td>7.51</td>
<td>0.57</td>
</tr>
<tr>
<td>P3</td>
<td>(37)</td>
<td>8.09</td>
<td>0.46</td>
</tr>
<tr>
<td>P4</td>
<td>(33)</td>
<td>8.42</td>
<td>0.52</td>
</tr>
<tr>
<td>M1</td>
<td>(45)</td>
<td>11.11</td>
<td>0.49</td>
</tr>
<tr>
<td>M2</td>
<td>(31)</td>
<td>10.76</td>
<td>0.57</td>
</tr>
</tbody>
</table>

<sup>a</sup> Computed by the formula: 100 - [100 x (min. mean/max. mean)].
<sup>b</sup> \( p < 0.05 \) (Student's t-test).
<sup>c</sup> \( p < 0.01 \) (Student's t-test).
Fig. 5-1. Comparison of preadult and adult tooth size differences (preadult mean – adult mean) (* = $p < 0.05$; ** = $p < 0.01$).

TABLE 5-2
Percent of Preadult and Adult Santa Catalina de Guale Individuals with at least One Hypoplasia

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Preadult</th>
<th>Adult</th>
<th>Percent difference*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
<td>N</td>
</tr>
<tr>
<td>Mandibular</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>(34)</td>
<td>44</td>
<td>(47)</td>
</tr>
<tr>
<td>I2</td>
<td>(33)</td>
<td>55</td>
<td>(56)</td>
</tr>
<tr>
<td>C</td>
<td>(48)</td>
<td>81</td>
<td>(90)</td>
</tr>
<tr>
<td>Maxillary</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>(29)</td>
<td>69</td>
<td>(53)</td>
</tr>
<tr>
<td>I2</td>
<td>(31)</td>
<td>77</td>
<td>(46)</td>
</tr>
<tr>
<td>C</td>
<td>(45)</td>
<td>85</td>
<td>(85)</td>
</tr>
</tbody>
</table>

* Adult % – preadult %.

None of these differences show statistical significance (Student’s $t$-test: all values of $p > 0.05$).

DISCUSSION

Stress has been studied in a variety of anthropological contexts, including determination of relative importance of the extrinsic stressors of certain elements of the group, and the identification of stress inducing or stress reducing phenomena (Brown, 1981). Broadly defined, stress can be considered to be the friction between an individual and his social, physical, nutritional, and disease environ-
Fig. 5-2. Comparison of preadult and adult age distribution of hypoplasia area (mandibular teeth).
Fig. 5-3. Comparison of preadult and adult age distribution of hypoplasia area (maxillary teeth).
ment. Such stressors are assumed to elicit a stereotypic, nonspecific physiological response for adaptive activity in the body "which includes the activation of homeostatic mechanisms" (Selye, 1956). The adaptive response to stressors includes increased cardiac output and respiratory activity, dilation of the blood vessels of the skeletal muscles, increased alertness and desensitization to pain, the sum of which increases the capability of the body in dealing with external stressors.

Although the stress response is initially adaptive, exposure to severe chronic or acute stress overloads the body's ability to continually and successfully adapt to the proximate and causative stressors, thereby leading to a detrimental biological response. It has been shown that chronic or prolonged stress leads to a variety of maladaptive physiological responses, including reduced resistance to disease (Selye, 1956; Stini, 1969), decreased fertility (Arvay, 1969), and retardation of growth (Kowarski et al., 1968; Frisancho et al., 1977).

Physiological disruptions in the hard tissues are a result of a rerouting of essential nutrients from growth processes to maintenance functions in response to disease or dietary stress (Cohen and Hansen, 1962). A number of physiological, developmental, and morphological anomalies resulting from periods of stress have been documented, including decreased stature (Acheson, 1960), enamel defects (Sarnat and Schour, 1941, 1942; Molnar and Ward, 1975; Rose, 1977; Garn et al., 1979), Harris (growth arrest) lines (Acheson, 1960; Garn and Schwager, 1967; Garn et al., 1968; although see Mensforth, 1985), reduced vertebral neural canal dimensions (Clark et al., 1986), and growth retardation in general (Tanner, 1962; Stini, 1969; Frisancho and Baker, 1970; Garn et al., 1979; Cook and Buikstra, 1979; Larsen, 1982, 1984; Cohen and Armelagos, 1984; and many others) in a variety of human groups, both past and present.

Physiological stress indicators have additional interpretive value because they are readily quantifiable, they are comparable across ethnic and cultural boundaries, and they are reasonably representative of ambient stress levels (Brown, 1981). The proximate stressor may vary across cultures, but the stress response does not. Therefore, stress level measurements are thought to be comparable between human groups with a wide temporal and spatial diversity as an indication of their respective stress loads and degree of biocultural integration.

The study of age-at-death and dental stress indicators has suggested that there is a non-random co-occurrence between the two. For example, Rose and co-workers (1978), Goodman and co-workers (1983), and White (1978) examined widely different dental samples, yet all observed that individuals exhibiting one or more enamel defect tended to have a younger age-at-death than individuals not exhibiting one or more enamel defects.

Some individuals within a population might not experience the same kinds of stressors or degrees of stress that affect mortality as others. Weanlings, for example, face an age-specific and generally traumatic suite of stressors during the dietary transition between maternal dependence and postweaning diet. Food sources other than mothers' milk are generally less sanitary and of poorer nutritional quality, thus leading to diarrhea, reduced host resistance, and metabolic and growth disruptions (Scrimshaw, 1964; Gordon et al., 1963). The nutritional needs of a one-year-old are roughly 150 percent of those of a three-year-old (Whitney and Hamilton, 1981). Co-occurring with the needs of the infant are dramatically increased nutritional needs of the mother.
TOOTH SIZE: Because of the high degree of heritability in teeth, a number of theoretical models based primarily on selective factors have been proposed to explain smaller teeth in the younger age-at-death categories in human populations. Perzigian (1975), for example, suggested that individuals with smaller teeth were selected out of the population as a result of an inability to attain a critical tooth size necessary to resist attrition. That is, smaller-toothed individuals were relatively less fit than larger-toothed individuals, thereby resulting in a greater mortality rate for the smaller-toothed individuals. This hypothesis appears unlikely because the reduction of crown breadth by substantially less than a millimeter will not automatically and inexorably lead to mortality. If the selective intensity was great enough to maintain a minimal crown area, then what factors explain the great amount of size overlap between the two age-at-death cohorts?

Undoubtedly, in the contact period population at Santa Catalina, disease resistance was under a very great selective intensity, particularly in light of the great magnitude of Native American mortality at this time. One can suggest that although the co-occurrence of larger teeth and immunological competence or successful stress mitigation cannot be denied, the probability that tooth size and disease resistance are somehow genetically linked in some fashion (pleiotropy) is low. That is, because both traits are polygenic, the amount of residual overlap may be insignificant. However, because they are polygenic traits, this is not possible to prove. Regardless, the mechanisms of selection most likely act very differently on each character. Hence, the implication that small teeth and poor disease resistance are genetic aliases of one another is not valid.

It is well known that tooth crown size is sexually dimorphic: females have smaller dental dimensions than males (Larsen, 1982; Frayer and Wolpoff, 1985; and others). Therefore, the possibility remains that smaller tooth crowns in the preadult cohort may be due not to an inability of those younger individuals to reach their genetic growth potential, but rather, the presence of more females in this group than in the adult cohort. In this regard, Stinson (1985) has reviewed evidence for sex-specific mortality rates. That is, there is some evidence that females may exhibit a greater relative mortality rate in very stressed environments due to cultural preference for keeping males alive and not females. Both Perzigian (1975) and Guagliardo (1982) have proposed that the differences that they noted between preadult and adult tooth size could be due to differential sex composition.

The poor skeletal preservation in part of the Santa Catalina cemetery precluded sex determination for many of the adults in the skeletal series. Of the 431 individuals recovered in the cemetery, it was possible to determine sex for less than 20 percent of the adult cohort. Therefore, it is not possible to examine potential biasing effects of sex ratio in this skeletal series. However, the lack of significant imbalance in sex composition in other skeletal series that have been examined demographically would suggest that a disproportionate number of females in the preadult component of the population does not exist (cf. Acsádi and Nemeskéri, 1970; Owlsley and Bass, 1979; Mensforth, 1986; and others). We suspect, therefore, that sex bias is not a major factor in interpreting these results.

The relative completeness of the dental samples in this study should be also considered as a potential bias factor. Figure 5-4 illustrates the dental completeness of the tooth size samples. Tooth representation at Santa Catalina is similar between the preadult and the adult groups. The only marked differences are seen in the mandibular central incisor and first molar and the maxillary second molar. Overall it appears that tooth type completeness does not bias preadult-adult differences.

Although sampling bias may influence estimation of preadult and adult tooth size, it is considered to be of little significance in the explanation of tooth size differences reported here. Therefore, metabolic disruption during the period of dental growth is considered to be the primary factor in explaining these differences. Despite the apparent strength of this relationship, it cannot be used in a predictive sense due to the great natural variation in tooth crown size and morphology as well as a general lack of understanding regarding the factors which contribute to tooth size.

Our findings of relative smaller preadult
tooth size in this population are consistent with those reported from other regions where stress is documented. With regard to the aforementioned study by Guagliardo (1982), for example, a comparison of preadult and adult tooth size in dental series from Tennessee (Averbuch site) and South Dakota (Larson site) revealed differences in preadult and adult tooth size. Both series are representative of late prehistoric or historic period populations experiencing elevated stress levels, and like the series from St. Catherines Island, most tooth types are smaller in preadults than in adults. Interestingly, both the comparisons reported by us and by Guagliardo (1982) show that the greatest degree of size differences tend to be in the posterior, mandibular teeth. We are in agreement with Guagliardo (1982) that these tooth size differences reflect high levels of chronic stresses in the populations. Quite clearly, environmental stress plays an important part in the expression of ultimate tooth size in the growing individual (cf. Townsend and Brown, 1978).

**Enamel Hypoplasias:** If the relationship between an earlier onset of hypoplasia-producing events and a younger age-at-death is real and not simply an artifact of sampling (see below), then this relationship is of clear importance in understanding both timing of stress episodes and survivorship. Because all periods of dental development are not equally important in terms of subsequent development, disruptions occurring during certain periods of growth may predispose those individuals to later metabolic problems or reduce their ability to adequately meet future and novel changes in their environment. Unfortunately, the size and equality of this sample precludes such an in-depth analysis. Future work must rely on a more complete skeletal sample which is more fully censused in terms of demographic and epidemiological parameters.

Pinpointing an explanation for the different hypoplasia widths for the preadult and adult cohorts is problematical. If hypoplasia width represents an estimate of stress episode duration (cf. Sarnat and Schour, 1941; Blakey and Armelagos, 1985) or severity (see discussion in Hutchinson and Larsen, this volume), then what factors allow a coincident greater duration or severity? One explanation is that the individuals with the greater hypoplastic widths survived long periods of subnormal development. Therefore, individuals who could not adapt to increased environmental stress were selected out and entered the mortuary sample prior to the

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**DENTAL SAMPLE COMPLETENESS**

Fig. 5-4. Comparison of preadult and adult completeness of dental samples.
TABLE 5-4
Comparison of the Mean Tooth Crown Heights (in mm) for the Preadult and Adult Cohorts from Santa Catalina de Guale

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Preadult N</th>
<th>Preadult Mean</th>
<th>Adult N</th>
<th>Adult Mean</th>
<th>Percent difference a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandibular</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>(32)</td>
<td>8.8</td>
<td>(44)</td>
<td>7.3</td>
<td>-17.0 b</td>
</tr>
<tr>
<td>I2</td>
<td>(30)</td>
<td>9.9</td>
<td>(52)</td>
<td>7.8</td>
<td>-21.2 b</td>
</tr>
<tr>
<td>C</td>
<td>(43)</td>
<td>11.4</td>
<td>(84)</td>
<td>9.3</td>
<td>-18.4 b</td>
</tr>
<tr>
<td>Maxillary</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>I1</td>
<td>(24)</td>
<td>11.2</td>
<td>(49)</td>
<td>9.5</td>
<td>-15.2 b</td>
</tr>
<tr>
<td>I2</td>
<td>(27)</td>
<td>10.1</td>
<td>(43)</td>
<td>8.6</td>
<td>-14.9 b</td>
</tr>
<tr>
<td>C</td>
<td>(39)</td>
<td>10.9</td>
<td>(77)</td>
<td>9.1</td>
<td>-16.5 b</td>
</tr>
</tbody>
</table>

a Computed by the formula: 100 - [100 \times (min. mean/ max. mean)].

b \( p < 0.05 \) (Student's t-test).

termination of the stress episode or prior to the completion of the formation of their respective dental crowns. This interpretation parallels the study of Meindl and Swedlund (1977), which concluded that a population is made "stronger" as a whole after passage through a severe stress window.

Other nondevelopmental factors could lead to similar hypoplasia-onset profiles of the two cohorts. For instance, the absence of hypoplasias in the occlusal, or earliest developing, portion of the teeth in the older death cohort, may simply be due to attrition, and not the result of an absence of metabolic disruptions during this time. Age and attrition are strongly and positively correlated; therefore, the earliest age categories may not have been sampled in the adult cohort, and their underrepresentation may, therefore, be an artifact of wear.

If it can be shown that the differences of the mean tooth heights of the two cohorts are minor, then little or no information was lost through attritional processes, especially as it relates to age-of-onset of hypoplasia. With regard to the Santa Catalina series, occlusal surface wear should be considered in preadult/adults comparisons.

In the Santa Catalina sample, mean tooth crown heights (measured from the top of the tooth crown to the mesial aspect of the cementoenamel junction) are significantly greater in the preadult cohort than in the adult cohort (Student's t-test: \( p < 0.05 \)) (table 5-4). Percent differences in means in preadult and adult crown heights range from 14.9 percent (maxillary lateral incisor) to 21.2 percent (mandibular lateral incisor).

In light of the marked reduction in adult crown height, it is clear that hypoplasias arising during the earliest stages of crown development would have been obliterated by occlusal surface wear. Therefore, effects of attrition quite likely compromise the use of enamel hypoplasias in looking at questions of age-at-onset of defects.

The use of hypoplasia data is important, however, in considering the overall differences in frequency of teeth affected by defects in preadults and adults. As shown above, there is a consistently higher frequency of preadult individuals than adult individuals with at least one hypoplasia (table 5-2). It is possible that some of this variation might be explained by greater occlusal wear in adult teeth than preadult teeth, resulting in fewer hypoplasias in the former. Occlusal surface wear obviates the use of earliest appearance data of metabolic disturbance, although other data for hypoplasias located adjacent to the occlusal surface may be evaluated. Goodman and Armelagos have shown that within teeth there are "biological gradients in susceptibility to ameloblastic disruption" (1985a: 479), with the middle and cervical thirds of the dental crown generally responding more readily to metabolic insult than the occlusal third of the crown. This observation was supported by the work of Hutchinson (1986) on material from the Georgia coast. Although one study reported that the occlusal third of the crown displays less than 33 percent of the total number of hypoplasias observed (13-22%, mean = 17.3% [Goodman and Armelagos, 1985a]), this is not an insignificant fraction of the total hypoplasia profile. By combining the effects of enamel attrition and differential crown susceptibility to metabolic insult, we can assess the effects of attrition in the older cohort and estimate the percentage difference in hypoplasia frequency which would merely reflect different ages of the cohorts. This percentage difference represents the null hypothesis value. In the Santa Catalina sample, the adult cohort would be expected to have 10 percent fewer hypoplasias than the
preadult cohort based on amount of enamel missing (20% in the adult cohort or 61% of the occlusal third of the crown) times the mean number of hypoplasias in the occlusal third of the anterior teeth (17%). Because this value either approximates or exceeds the observed differences, the null hypothesis cannot be rejected based on these findings.

In summary, the study of tooth size and enamel defects in the Santa Catalina series has demonstrated that metabolic disruption during the period of dental development leaves a legacy of subsequent growth alteration. These data suggest that teeth are important indicators of the health status of a population. Under the tenets of the null hypothesis, if the factors of mortality and ability to resist growth disruption were independent of each other, then the preadult and adult groups would have similar stress profiles. We suggest that this is not the case. Neither mortality factors nor the ability to resist exogenous stressors are random events. In this context, then, stress is a selective factor of evolution; mortality is one of its effects. The inability to lessen or cope with the ambient stressors indicates that these preadults were less fit in that environment. This does not imply that smaller teeth or more hypoplasias cause death or reduce survivorship, but rather that factors which cause widespread and generalized physiological and developmental disruptions, as indicated by smaller tooth crowns and a younger age-at-death, are intimately linked. Reduced survivorship and reduced growth potential result from the inability to mitigate the cumulative effects of the external stressors and this reflects the biological inability of those individuals to withstand the rigors of life.

CONCLUSIONS

This work compared the dental stress indicator profiles for preadult and adult cohorts for the Santa Catalina de Guale sample. The null hypothesis proposes that the stress indicator profiles for the two groups would be similar. The conclusion drawn from acceptance of the null hypothesis would be that factors of morbidity and mortality, with their concomitant suite of growth disruptions, are independent of each other. Analysis of tooth crown size data indicates, however, that the null hypothesis can be rejected because the adult cohort tends to have larger tooth crowns than the preadult cohort. Primarily because of factors associated with occlusal surface attrition, the hypoplasia results are more problematical. That is, frequency of affliction, width of stress events, and timing of hypoplasia onset data are not sufficient to reject the null hypothesis.

Nondevelopmental or sampling factors undoubtedly contributed to the differences observed in the hypoplasia profiles between cohorts. However, a developmental explanation of crown size variation between the age groups seems to be the most parsimonious of the alternative hypothesis. Overall, these data support the contention that the ability to resist metabolic insult has an effect on subsequent survivorship, thus demonstrating a dependent relationship between these factors.

ACKNOWLEDGMENTS

An earlier version of this paper was presented at the 1986 annual meetings of the American Association of Physical Anthropologists and the Paleopathology Association held in Albuquerque, New Mexico. The research for this paper was supported by grants from the St. Catherines Island Foundation and the National Science Foundation (award BNS-8406773). We thank Ms. Lisa L. Goscielow and Ms. Prisca Kolkowski for preparation of the artwork.
CHAPTER 6. DECREASE IN DIET QUALITY BETWEEN THE PREHISTORIC AND THE CONTACT PERIODS

MARGARET J. SCHOENINGER, NIKOLAAS J. VAN DER MERWE, KATHERINE MOORE, JULIA LEE-THORP, AND CLARK SPENCER LARSEN

ABSTRACT

Archaeological data indicate that for most of prehistory, Georgia coastal native populations focused on wild foods that were extracted from both terrestrial and marine environments. By the later part of prehistory (12th century A.D.), maize agriculture provided an important component of diet. This dietary shift involved, then, the incorporation of a relatively poor quality nutritional resource. This paper presents data on stable isotopic ratios of carbon and nitrogen in bone organic residues (collagen) to indicate certain components of diet in prehistoric and contact period Georgia coastal populations. Three subsamples are examined: (1) precontact preagricultural (Refuge-Deptford and St. Catherines periods), (2) precontact agricultural (Savannah period); and (3) contact agricultural (mission period).

There is a clear trend for lower $\delta^{15}$N values and higher $\delta^{13}$C values in the precontact agricultural and contact periods compared with the precontact preagricultural periods. These data indicate an overall decrease in marine foods (primarily molluscs and fish) and an increase in terrestrial foods, namely maize. Consistent with the archaeological record of dietary reconstruction (see Reitz, 1988), marine resources remain important dietary items late in prehistory as well as in the contact period. The use of a more limited repertoire of dietary items in concert with other stressors during later prehistory and in the contact period by native populations may have contributed to their extinction.

INTRODUCTION

As discussed in other chapters in this volume, various changes in subsistence strategy, settlement pattern, and health occurred among the human populations inhabiting St. Catherines Island throughout its nearly 4000 years of occupation. This paper concentrates on the dietary adaptations of both the prehistoric and postcontact inhabitants, which, in combination with the other studies in the St. Catherines Island project, should elucidate the interactions among these variables and provide a greater understanding of the final extinction of these populations.

The specific technique uses stable isotope ratios of carbon and nitrogen in bone organic residues (referred to in this paper as collagen) to indicate certain components in human diet. In most studies of this nature, the stable carbon isotope ratios in bone collagen are used to document the incorporation of maize into human diet (e.g., Vogel and van der Merwe, 1977; Bender et al., 1981). Along the Georgia coast, however, the potential dependence on marine foods, also reflected in stable carbon isotope ratios, confounds such direct application. The use of nitrogen stable isotope ratios as the primary indicator of marine foods permits use of carbon stable isotope ratios in monitoring the introduction of maize as an item in diet.

In order to determine whether or not changes in human diet correspond to changes evidenced by the archaeological record, human bone samples from cultural periods representing precontact preagricultural, precontact agricultural, and contact agricultural adaptations were analyzed. Although the general aspects of human subsistence activity along the Georgia coast are fairly well known (see discussions in Thomas, 1987; Reitz, 1988; Larsen, this volume), information about the percentages of particular diet components and the manner of change through time has not been determined. Such information is particularly important because of reported evidence from recovered human skeletons that changes in behavior and nutrition or both took place over this period of time (reviewed in Larsen, this volume). The significant decrease in skeletal robusticity
(Ruff et al., 1984) and the increase in incidence of skeletal pathologies related to mechanical stress (Larsen, 1982) suggest behavioral changes associated with evidence for maize agriculture. Intimations of changes in the adequacy of the nutritional base are (1) the increased frequency of certain infectious diseases (Larsen, 1982); (2) the presence of tuberculosis and nonvenereal treponematosis at the Irene Mound site (Powell, this volume); (3) the increased stress as indicated by abnormal enamel formation patterns (Hutchinson and Larsen, 1988, this volume; Hutchinson, 1986); and (4) the increased incidence of dental caries (Larsen, 1982).

It is not possible to tease apart the debilitating effects of infectious disease exacerbated by close living conditions from those effects brought about by nutritional stress. Yet, the overall effect of the interplay between diet and disease may account for the demographic data presented by Russell and co-workers (this volume; Russell, 1987). Dietary insufficiencies during the agricultural periods may explain some of these observations, for, as discussed elsewhere in this volume (Hutchinson and Larsen), maize is a notoriously poor protein source. Clearly, more specific information on diet is necessary.

This study provides an ideal test case for the use of stable isotope ratios of carbon and nitrogen in a situation in which marine foods were of major importance prior to the introduction of maize. As discussed in more detail below, use of carbon isotope ratios in coastal regions of the New World is not an accurate method of estimating the inclusion of maize in diets because the carbon isotope signature of marine foods (van der Merwe, 1982; Schoeninger and DeNiro, 1984) is equivalent to that produced by a partial maize diet. For this reason, an alternative indicator of use of marine foods is necessary in such cases. A previous study demonstrated that nitrogen isotopes can, in many instances, be used to distinguish between dependence on marine versus dependence on terrestrial foods (Schoeninger and DeNiro, 1984; Schoeninger et al., 1983). It was suggested that by using nitrogen isotope ratios to indicate marine food use, carbon could then be used to indicate maize use. The application has been attempted only once previously, in a very complicated and, therefore, less easily interpretable situation (Keegan, 1987). The present study is an ideal application because the baseline carbon and nitrogen isotope values can be established using precontact preagricultural period samples and then these values can be compared with those from precontact agricultural and contact period agricultural samples.

**DIETARY CONTEXT**

Prior to the introduction of maize agriculture in the Georgia coastal area, the inhabitants appear to have been foragers who depended on various wild foods extracted from both the marine and terrestrial environments (Larsen, 1982; Reitz, 1985, 1988). The Refuge period (1100–400 B.C.) is the earliest period for which skeletal remains are available. During parts of the period, shellfish were used, yet middens representing parts of the period are noted for their lack of shell, suggesting relatively little use of shellfish in diet. Marine and estuarine fish were collected throughout the period, although sea level varied from significantly lower than present to that of modern levels (DePrattter and Howard, 1977, 1978). This variation in sea level and concomitant reduced availability of certain molluscs has been proposed as an explanation for the presence of sites with different combinations of food remains (Larsen, 1982: 164). Among the land mammals, deer predominated, although smaller mammals such as raccoon, rabbit, and squirrels were also hunted. Several plant species were used, most commonly hickory and acorns. Hickory nuts may have been processed for oil while the acorns were eaten as a bread (Larson, 1980; Hann, 1986b).

The succeeding Deptford period (400 B.C.–A.D. 500) appears to have included subsistence opportunities similar to those available during the Refuge period. Sea level had reached the modern level, and a large variety of marine and estuarine fish, molluscs, and even some sea mammals were exploited. In addition, deer and other mammals, plus acorn and hickory continued to be included as diet items (Thomas and Larsen, 1979).

The same general picture continued in the last two preagricultural periods, the Wil-
mington period (A.D. 500–1000) and the St. Catherines period (A.D. 1000–1150). Larsen (1982) has noted, however, that few data on plant and animal remains have been reported from sites dating to either period. Available data suggest that the same regime appears to have been followed, although it is interesting to note that at some sites most of the animal remains are molluscs.

In sum, the precontact preagricultural subsistence economy of the people inhabiting St. Catherines Island and the Georgia coast appears to have focused on the collection of marine, estuarine, and terrestrial fauna. The availability of molluscs varied according to sea level during the earliest period considered in this study. Plant foods consisted mainly of acorn and hickory nuts. A summary of plant food remains found in the Southeast (Yarnell and Black, 1985) includes four cultigens (squash, bottle gourd, sunflower, and sumpweed) and several small grains (millet, knotweed, Chenopodium, and amaranth). There appears to be no evidence of “gardening” in the Georgia coastal area prior to maize agriculture, nor have significant remains of the small grains been reported from this region. The most recent discussions of food production in the Southeast report no evidence contradicting this statement (Ford, 1985; Smith, 1986; Steponaitis, 1986). Larsen (1982: 167) has maintained that the sites from these periods “represent isolated short-term occupations.” A recent overview of the seasonality of shellfish use along the Georgia coast supports this opinion (Claassen, 1986a).

Evidence for maize agriculture first appears on the Georgia coast during the two cultural periods following the St. Catherines period. Also, during these two periods, Savannah period (A.D. 1150–1300) and the Irene period (A.D. 1300–1550), a change occurred in settlement pattern (Larsen, 1982, this volume). Sites are larger, and Larsen (1982) has suggested that human populations were more sedentary than in the earlier periods. These dietary and settlement changes are consistent with other developments in eastern North America that are associated with the Mississippian period in general.

With the exception of maize, however, the same foods appear as were used previously. Reitz (1985) reported a continued emphasis on fish, especially small fish which would have been collected in the marshes. This use of shallow water resources is also indicated by the recovery of marsh-edge turtles and molluscs in sites dating to these periods (Reitz, 1985, 1988). Other evidence indicates that oysters, always the most abundant mollusc species recovered in middens, became even more important during the Savannah and succeeding periods (Claassen, 1986b). It is possible that this reflects intensification of exploitation of molluscs in general (Larsen, this volume; Quitmyer et al., 1985). Few birds were taken by the aboriginal inhabitants, and Reitz (1985) suggested that only with the introduction of Spanish firearms was bird capture an energy efficient activity. Among terrestrial mammals, deer continued to be the most common.

Thus, the precontact agricultural periods display the same mix of food items as was available before the introduction of maize agriculture. There may have been some increased dependence on molluscs (particularly oysters) relative to other fauna. The level of dependence on maize has not been estimated, but maize has been recovered from sites dating to the precontact agricultural Savannah and Irene periods.

The contact (Spanish) period (post-A.D. 1550) follows the Savannah and Irene periods. By 1576, a town with a mission had been established on St. Catherines Island (Jones, 1978). The populace probably included the descendants of earlier inhabitants of the island, and also people from the mainland who had been moved there at the direction of the Spanish (Larsen, this volume; Thomas, 1988). Bushnell (1987), Loucks (1979), and others have pointed out that the populations associated with a number of the missions, including Santa Catalina de Guale, were required to supply the Spanish with maize. Further, Reitz (1985) has suggested that the decrease in relative quantity of deer bones recovered from middens in areas of Spanish Florida can be explained by trade of deer to the Spanish resulting in a decrease in use of deer by the contact period natives. She also noted that none of the European domesticates, plants or animals, were of great importance to the native inhabitants along the Georgia coast (Reitz and Scarry, 1985;
Reitz, 1987). They continued using the plants (maize, acorn, hickory) and animals (deer and molluscs) on which they depended prior to the incursions by the Spanish. Fauna recovered from Santa Catalina shows an unusually high percentage of deer (Duncan, 1987). These remains, however, quite likely reflect European diet at this mission rather than native diet (Reitz, 1988).

MATERIALS AND METHODS

SAMPLES: The samples analyzed are listed in table 6-1 by cultural period. Individuals from the precontact preagricultural Refuge and Deptford periods have been combined into a single sample because it was not possible to attribute individuals to one or the other period with any accuracy (Thomas and Larsen, 1979). No samples were available from the Wilmington period on the island; therefore, this period is not represented in the present study. Human skeletal material which can be assigned to the earliest agricultural period on the island (the Savannah period) was also not available for analysis. Because it was extremely important to analyze individuals from this cultural period, bone from a burial locality at the Irene Mound site known as "The Burial Mound" was analyzed. This locality dates primarily from the Savannah period component of the Irene Mound site (A.D. 1150–1300) (Caldwell and McCann, 1941).

Some differences in subsistence procurement may have occurred between the Irene Mound site and St. Catherines, but they were probably minor. In fact, it is probable that the preagricultural St. Catherines Island and the agricultural Irene Mound inhabitants were related biologically. Several lines of evidence presented by Larsen (1982) support this contention. First, prior to the Savannah period (before A.D. 1150), most sites are small and widely dispersed, probably representing short-term occupations. During the later Savannah and Irene periods (after A.D. 1150), many of the sites are large and the deposits are significantly deeper than those of the earlier periods. It appears as if some consolidation or increase in population had occurred. Consolidation would have entailed movement of people from smaller habitation areas to large ones like Irene. Second, the ethnohistory of the region indicates that at the time of the earliest Spanish contact, the Georgia coast and its barrier islands were part of a consortium of interacting towns. In all likelihood, this interaction occurred during the Savannah and Irene periods as well. Taken together, it is most reasonable to assume that the populations on St. Catherines and those on the mainland coastal region of Georgia had similar subsistence/dietary adaptations because they were all part of a single large population.

The human bone samples in table 6-1 which have been assigned to the contact period were recovered from Santa Catalina de Guale. These skeletons represent people from the mainland who were moved to the island, people living on the island at the time the mission was established, and people born on the island following the establishment of the mission. Analysis of pottery (discussion in Larsen, 1982) shows that the contact populations and their prehistoric forebears were likely from the same population. That is, there are no sudden breaks in either method of ceramic production or style, suggesting little or no migration of populations from regions outside of the Georgia coast until the arrival of Europeans and movement of native populations during the later decades of the Spanish period.

DIET ESTIMATION: The relative importance of different plants and animals in a diet is difficult to assess from the remains of those food items recovered from archaeological sites (Smith, 1979). Although plant or animal foods may often be ranked in importance based on their abundance in middens, it is impossible to measure the dietary importance of plant foods relative to animal foods overall. This is true particularly in cases like the present where the list of diet items (with the exception of maize) remained the same throughout the period of native occupation. Information on certain aspects of dietary composition can, however, be obtained by analysis of the stable isotope composition of the organic material in bone.

The stable carbon isotope ratio ($^{13}$C/$^{12}$C) in an animal's bone collagen reflects the isotopic composition of that animal's diet. This relationship has been demonstrated by a se-
### TABLE 6-1
Georgia Coastal Bone Samples for Isotopic Analysis

<table>
<thead>
<tr>
<th>Period</th>
<th>Lab no.</th>
<th>Site</th>
<th>$\delta^{13}$C (PDB)%o</th>
<th>$\delta^{15}$N (AIR)%o</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precontact preagricultural</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Refuge-Deptford</td>
<td>UCT 386</td>
<td>Seaside Md. II</td>
<td>-13.8</td>
<td>10.6</td>
</tr>
<tr>
<td></td>
<td>388</td>
<td></td>
<td>-13.4</td>
<td>13.2</td>
</tr>
<tr>
<td></td>
<td>389</td>
<td>McLeod Md.</td>
<td>-17.1</td>
<td>13.1</td>
</tr>
<tr>
<td></td>
<td>391</td>
<td></td>
<td>-18.6</td>
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<td>12.6</td>
</tr>
<tr>
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<td>393</td>
<td></td>
<td>-13.6</td>
<td>12.4</td>
</tr>
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<td></td>
<td>394</td>
<td>Cunningham Md. C</td>
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<td>14.4</td>
</tr>
<tr>
<td></td>
<td>396</td>
<td>Cunningham Md. D</td>
<td>-13.9</td>
<td>12.9</td>
</tr>
<tr>
<td>St. Catherines</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>370</td>
<td>Johns Md.</td>
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<td></td>
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<td>374</td>
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<td>12.3</td>
</tr>
<tr>
<td></td>
<td>375</td>
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<td>-14.4</td>
<td>12.7</td>
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<td></td>
<td>376</td>
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</tr>
<tr>
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<td></td>
<td>-14.3</td>
<td>13.5</td>
</tr>
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<td>379</td>
<td></td>
<td>-13.4</td>
<td>13.1</td>
</tr>
<tr>
<td></td>
<td>380</td>
<td>Marys Md.</td>
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<td>11.8</td>
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<td></td>
<td>381</td>
<td></td>
<td>-14.7</td>
<td>12.9</td>
</tr>
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<td>Precontact agricultural</td>
<td>UCT 349</td>
<td>Irene Md.</td>
<td>-14.0</td>
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</tr>
<tr>
<td></td>
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<td>-13.3</td>
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<td>-11.5</td>
<td>13.3</td>
</tr>
<tr>
<td>Contact agricultural</td>
<td>MS 2835</td>
<td>Santa Catalina</td>
<td>-9.6</td>
<td>7.4</td>
</tr>
<tr>
<td>Mission</td>
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<td></td>
<td>2836</td>
<td></td>
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<td></td>
<td>-14.3</td>
<td>9.5</td>
</tr>
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</table>
Table 6-1 (Continued)

<table>
<thead>
<tr>
<th>Period</th>
<th>Lab no.*</th>
<th>Site</th>
<th>δ13C (PDB)‰</th>
<th>δ15N (AIR)‰</th>
</tr>
</thead>
<tbody>
<tr>
<td>Modern fauna</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-tailed deer</td>
<td>MS 2768</td>
<td>St. Catherines Island</td>
<td>-22.2</td>
<td>4.4</td>
</tr>
<tr>
<td>Catfish</td>
<td>2779</td>
<td></td>
<td>-11.4</td>
<td>11.6</td>
</tr>
<tr>
<td>Loggerhead turtle</td>
<td>2776</td>
<td></td>
<td>-14.9</td>
<td>10.5</td>
</tr>
<tr>
<td>Archaeological plant</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maize</td>
<td>MS 3074</td>
<td>Santa Catalina</td>
<td>-12.1</td>
<td>2.2</td>
</tr>
</tbody>
</table>

*UCT refers to samples analyzed at the University of Cape Town; MS refers to samples analyzed at Harvard University.

ries of controlled laboratory studies (DeNiro and Epstein, 1978; Bender et al., 1981; Tieszen et al., 1983). Because the concentration of
13C in the biosphere is very low, the ratio (13C/12C) cannot be measured directly. Rather,
in the manner followed in this paper, the ratio is represented as a delta (δ) value in parts
per thousand (read as “per mil,” represented by the symbol ‰). This value is the result of
comparing the isotope ratio in the sample with the same ratio in a nationally recognized
standard. The equation is shown below:

δ13C = \left[ \frac{(13C/12C)_{sample}}{(13C/12C)_{standard}} - 1 \right] \times 1000‰

*standard = Peeedee belemnite (PDB) carbonate

The carbon stable isotope ratio in bone coll-
gen is not identical to the diet isotope ratio. Rather, a fractionation occurs between diet
and bone collagen. This fractionation results in a δ13C value in bone collagen that is more
positive (less negative) than the value in diet. There remains some uncertainty concerning
the actual magnitude (Vogel, 1978 versus DeNiro and Epstein, 1978 and Bender et al.,
1981), and whether or not the fractionation factor is constant across all diets (Bumsted,
1983, 1984). For the purposes of this study, however, we can assume constancy, because
the expected variation across diets is not large enough to effect any change in the magnitude
of the fractionation factor. In making rough estimates of diet composition, the fractiona-
tion factor is assumed to be 5‰ as observed in field studies (Vogel, 1978) and as is
commonly used in human diet studies.

The δ13C value of bone collagen has been demonstrated to separate two major dietary
categories. The first distinction is between two groups of plants which follow separate pho-
tosynthetic pathways and differ significantly in the amount of 13C incorporated in their
tissues. C4 plants (tropical grasses such as maize) and consumers of C4 plants have δ13C
values that differ by about 14‰, on average, from those of C3 plants (the majority of leafy
plants) and consumers of C3 plants (Bender, 1971; Smith and Epstein, 1971; DeNiro and
Epstein, 1978; Vogel, 1980; O’Leary, 1981). This difference is reflected in the bone col-
lagen of people who obtain their calories from one or the other category (van der Merwe
et al., 1978; van der Merwe, 1982; Land et al., 1980; Schoeninger et al., 1983; Bumsted,
1984). Because of this relationship, δ13C values have been used successfully to monitor
the introduction of maize agriculture into interior mainland areas of the New World (Vo-
gel and van der Merwe, 1977; van der Merwe and Vogel, 1978; van der Merwe et al.,
1981; Bender et al., 1981; Farnsworth et al., 1984; Schwarcz et al., 1985; Lynott et al.,
1986; Buikstra et al., 1987; and Keegan, 1987).

The second major category of diet indi-
cated by δ13C values is the inclusion of marine
foods. Marine fish and mammals have δ13C
values that are more positive by about 6‰,
relative to terrestrial animals feeding on C3-
based foods and about 7‰ less positive than
terrestrial animals feeding on C4 (maize)-
based foods (Schoeninger and DeNiro, 1984;
Schoeninger et al., 1983). In other words, ma-
rine animals have δ13C values that fall be-
tween the two extremes represented by C3-
and C4-based food chains. In areas in which
maize or other C4 plants are not eaten by
humans, the δ13C value of human bone col-
lagen has been used to indicate the inclusion
of marine foods in human diet (Tauber, 1981;
Chisholm et al., 1982; Schoeninger et al.,
1983; Hobson and Collier, 1984; Sealy and
van der Merwe, 1986). On the Georgia coast,
maize was introduced into a diet which included a significant amount of marine foods. Identical bone collagen $\delta^{13}C$ values could be produced from a diet of 90% marine food and 10% C3-based food as well as a diet of 50% maize and 50% C3-based food. For this reason, it is not possible to use $\delta^{13}C$ values, in isolation, to monitor the introduction of maize into the Georgia coast. Nitrogen isotope ratios are used to clarify the situation.

As with carbon, both field studies (Wada, 1980; Wada et al., 1975; Wada and Hattori, 1976) and controlled feeding experiments (DeNiro and Epstein, 1981; Fogel, personal commun.) demonstrated that the $^{15}N/^{14}N$ ratio in an animal's tissues (including bone collagen) reflects the $^{15}N/^{14}N$ ratio of the animal's diet. As is true for $^{13}C$, the concentration of $^{15}N$ in the biosphere is very low, thus, the results of the analyses are presented as delta ($\delta$) values in parts per mil (‰) as shown below:

$$\delta^{15}N = \left[ \frac{^{15}N/^{14}N_{\text{sample}}}{^{15}N/^{14}N_{\text{standard}}} - 1 \right] \times 1000 \text{‰}$$

*standard = Atmospheric Nitrogen (AIR)

As with carbon isotope ratios, the bone collagen nitrogen isotope ratio is not identical to the diet nitrogen isotope ratio. A fractionation of 2.5–3.0‰ occurs which results in the bone collagen having more positive delta values than those found in diet.

In many geographical regions, the $\delta^{15}N$ values of terrestrial organisms differ from the values in marine organisms by about 10‰ on average (Schoeninger and DeNiro, 1984). In these areas, the $\delta^{15}N$ value of bone collagen can be used to determine the use of marine foods by human groups (Schoeninger et al., 1983). A preliminary analysis of marine and terrestrial fauna from St. Catherines Island (see table 6-1) confirmed that the Georgia coast is an area in which stable nitrogen isotope ratios distinguish between marine and terrestrial food sources.

Therefore, the nitrogen stable isotope ratio in human bone collagen can be used to estimate the dependence on marine foods by the populations along the Georgia coast who also practiced maize agriculture. Thus, if the nitrogen isotope ratio becomes less positive through time (indicating increasing dependence on terrestrial foods), or remains constant, but the carbon isotope ratio becomes more positive through time, then it can be concluded that maize has been included as a diet item (see fig. 6-1). We expect that the preagricultural populations will fall somewhere along the line shown in figure 6-1. The exact placement will depend on the actual mix of dietary items. In the agricultural periods, we expect to see values along a line connecting the preagricultural position and "C4—no marine" in figure 6-1.

**Sample Preparation and Analysis:** Organic material was extracted from bone following the procedures used previously (Schoeninger and DeNiro, 1984; Sealy and van der Merwe, 1986). Only bone samples with organic residues that were over 5 percent of the original bone weight (fresh bone yields about 25% organic residue) and that had atomic carbon : nitrogen ratios between 2.7 and 3.3 were analyzed. Bone samples with lower percentage organic and different C:N ratios have been shown to have delta values that are not reflective of biological values (Schoeninger and DeNiro, 1982; DeNiro, 1985). For the contact period, 66 human bone samples were prepared. Of these, only 22 had over 5 percent organic material and had C: N ratios in the acceptable range. Collagen samples were combusted using a modified version of the Stump and Frazer (1973) method (Northfelt et al., 1981). The resulting CO$_2$ and N$_2$ were separated and purified in a vacuum system by cryogenic distillation prior to determination of their isotope ratios by mass spectrometry.

Samples from the precontact preagricultural Refuge-Deptford and St. Catherines periods and the precontact agricultural Savannah periods were analyzed in N. J. van der Merwe's laboratory at the University of Cape Town. The samples from the contact period were analyzed in M. J. Schoeninger's laboratory at Harvard University.

As a general interlaboratory comparison unrelated to this project, a set of bone samples from the Georgia coast dating to the Deptford period (not the samples reported in this study) was analyzed at the University of California in Los Angeles (U.C.L.A.) and at


THEORETICAL MODEL

![Graph showing values expected theoretically in human bone collagen from each of three diets. The first with low nitrogen and low carbon values would be produced from a diet of terrestrial foods all of which have C3 plants at the base of the food chain. The second, with high nitrogen and intermediate carbon values, would be produced from a diet of marine foods. The third, with low nitrogen and high carbon values, would be produced from a diet of terrestrial foods, all of which have C4 plants at the base of the food chain. Based on the archaeological evidence from the Georgia coast, we expect to find the human sample from preagricultural periods to fall somewhere along the line connecting the first two model diets. Further, we expect that the agricultural humans should plot somewhere along a line connecting the first line with the third model diet (see text for explanation).](image)

The results demonstrate that isotope ratios from bone collagen produced by the two labs are identical within acceptable limits (tables 6-2 and 6-3).

In addition, three bone samples from a previous study (Schoeninger et al., 1983) and several standards were analyzed at both the University of California in Los Angeles and Harvard University. The similarity of these results (tables 6-2 and 6-3) demonstrates that analyses from the U.C.L.A. and Harvard laboratories can be compared directly. Taken together, the isotope ratios produced by the three labs are directly comparable.

RESULTS

Results of this investigation are presented in tables 6-1, 6-4, and 6-5 and figures 6-2, 6-3, and 6-4. The set of samples from the two precontact preagricultural periods have average $\delta^{15}$N values which are virtually identical (see table 6-4). Even so, the range of values in the Refuge-Deptford period sample is large ($4\%$) relative to that previously ob-
### TABLE 6-2
Interlab Comparisons of Nitrogen Isotopic Analysis

<table>
<thead>
<tr>
<th>Lab</th>
<th>Sample</th>
<th>N</th>
<th>Mean</th>
<th>±SD</th>
<th>V, %</th>
<th>Range</th>
</tr>
</thead>
<tbody>
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<td><strong>Archaeological samples</strong></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>UCLA</td>
<td>Deptford site</td>
<td>6</td>
<td>10.2</td>
<td>1.3</td>
<td>12</td>
<td>8.3, 11.6</td>
</tr>
<tr>
<td>Cape Town</td>
<td>Deptford site</td>
<td>10</td>
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<tr>
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<td>Harvard</td>
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<td>-1.3</td>
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<td>17</td>
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<td>-</td>
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<td>Peptone</td>
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<td>7.0</td>
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<td>1</td>
<td>12.4</td>
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<td>-</td>
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<td>15.6</td>
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<tr>
<td>UCLA</td>
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<td>16.5</td>
<td>-</td>
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</tr>
<tr>
<td>Harvard</td>
<td>Bowhead whale 2</td>
<td>1</td>
<td>17.2</td>
<td>-</td>
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</table>

<sup>a</sup> Taken from Nevins et al., 1985.
<sup>b</sup> Represents replication of UCLA samples prepared and analyzed at Harvard.

### TABLE 6-3
Interlab Comparisons of Carbon Isotopic Analysis

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<thead>
<tr>
<th>Lab</th>
<th>Sample</th>
<th>N</th>
<th>Mean</th>
<th>±SD</th>
<th>V, %</th>
<th>Range</th>
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<td>Deptford site</td>
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<td>1.3</td>
<td>8</td>
<td>-16.9, -13.5</td>
</tr>
<tr>
<td>Cape Town</td>
<td>Deptford site</td>
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<td>-15.9</td>
<td>1.9</td>
<td>12</td>
<td>-18.6, -12.6</td>
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<td><strong>Standards</strong></td>
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<td>UCLA</td>
<td>Thiourea</td>
<td>27</td>
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<td>1</td>
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<td>UCLA&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>Harvard</td>
<td>Peptone</td>
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<td>-14.9</td>
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<td>-15.0, -14.6</td>
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<td>UCLA</td>
<td>Pig bone standard</td>
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<td>0.1</td>
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<td>-12.6, -12.4</td>
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<tr>
<td>Harvard</td>
<td>Pig bone standard</td>
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<td>-12.6</td>
<td>-</td>
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</tr>
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<td><strong>Modern samples</strong></td>
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<td></td>
</tr>
<tr>
<td>UCLA&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Walrus</td>
<td>1</td>
<td>-13.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Harvard</td>
<td>Walrus</td>
<td>1</td>
<td>-13.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>UCLA</td>
<td>Bowhead whale 1</td>
<td>1</td>
<td>-16.4</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td>Harvard</td>
<td>Bowhead whale 1</td>
<td>1</td>
<td>-16.5</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>UCLA</td>
<td>Bowhead whale 2</td>
<td>1</td>
<td>-15.3</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Harvard</td>
<td>Bowhead whale 2</td>
<td>1</td>
<td>-15.3</td>
<td>-</td>
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</tr>
</tbody>
</table>

<sup>a</sup> Carbon not reported by Nevins et al., 1985.
<sup>b</sup> Represents replication of UCLA samples prepared and analyzed at Harvard.
Nitrogen Isotopic Analysis Summary Statistics

<table>
<thead>
<tr>
<th>Period</th>
<th>N</th>
<th>Mean</th>
<th>±SD</th>
<th>%</th>
<th>Range</th>
</tr>
</thead>
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<tr>
<td>Precontact preagricultural</td>
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<td></td>
<td></td>
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<tr>
<td>Refugee-Deptford</td>
<td>8</td>
<td>12.7</td>
<td>1.0</td>
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<tr>
<td>St. Catherines</td>
<td>12</td>
<td>12.8</td>
<td>0.6</td>
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<td>11.6, 13.6</td>
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<tr>
<td>Precontact agricultural</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savannah</td>
<td>9</td>
<td>10.7</td>
<td>1.1</td>
<td>11</td>
<td>9.5, 13.3</td>
</tr>
<tr>
<td>Contact agricultural</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Mission</td>
<td>22</td>
<td>9.4</td>
<td>0.8</td>
<td>8</td>
<td>7.4, 10.8</td>
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<tr>
<td>Moderna</td>
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<td></td>
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<td></td>
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<tr>
<td>Eskimo</td>
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<td>18.1</td>
<td>0.8</td>
<td>4</td>
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<td>Pueblo</td>
<td>11</td>
<td>8.0</td>
<td>1.5</td>
<td>18</td>
<td>5.8, 11.5</td>
</tr>
</tbody>
</table>

* Taken from Schoeninger et al., 1983.

served in animals on monotonous diets (2‰: DeNiro and Schoeninger, 1983). The range of δ¹⁵N values in the subsequent preagricultural St. Catherines period is smaller (2‰), and we interpret this as representing a greater homogeneity in diet (and, we presume, adaptation) than was true for those individuals analyzed in the earlier period. It should be recalled that Refuge period middens vary in their contents, especially in the presence of molluscs. Further, the time represented by the combined Refuge and Deptford periods totals over 1500 years compared with 150 years in the St. Catherines period. It is likely that the individuals in the earlier sample represent various adaptations from different times within the precontact preagricultural period.

The carbon isotope ratios are more positive in the St. Catherines period relative to the Refuge-Deptford period (table 6-5). Although the difference, on average, is only 1‰, the range of values differs markedly. The range of values for carbon is much smaller within the St. Catherines period (1‰) than in the Refuge-Deptford period, similar to the pattern seen in nitrogen. It is possible that this represents sampling error; but more likely it reflects a more focused dietary adaptation within the short time span represented by the St. Catherines period (150 years). This range is similar to that reported previously for animals on monotonous diets (DeNiro and Schoeninger, 1983).

The human sample from the earliest agricultural period, the Savannah period, has more positive carbon delta values and less positive nitrogen delta values, on average, than in the preagricultural sample. Both trends suggest decreasing reliance on marine foods and increased reliance on terrestrial plants and animals. The coefficients of variation for both values are high (δ¹³C = 15%, δ¹⁵N = 11%) indicating that a variety of dietary adaptations were practiced during this period. The contact period sample shows a contin-

<table>
<thead>
<tr>
<th>Period</th>
<th>N</th>
<th>Mean</th>
<th>±SD</th>
<th>%</th>
<th>Range</th>
</tr>
</thead>
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<tr>
<td>Precontact preagricultural</td>
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<tr>
<td>Refugee-Deptford</td>
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<td>Eskimo</td>
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<td>-14.6</td>
<td>1.8</td>
<td>12</td>
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<tr>
<td>Pueblo</td>
<td>11</td>
<td>-8.0</td>
<td>0.9</td>
<td>11</td>
<td>-10.6, -7.3</td>
</tr>
</tbody>
</table>

* Taken from Schoeninger et al., 1983.
uncance of the trend of increasing carbon delta values and decreasing nitrogen delta values. The coefficients of variation are smaller in this sample relative to the Savannah period, but the range of values is larger than was observed in animals raised on monotonous diets.

DISCUSSION

GENERAL: Overall, there is an obvious trend of lower δ15N values and higher δ13C values in the precontact Savannah and the contact agricultural periods compared with the preagricultural periods (fig. 6-2). The decrease in δ15N values between the preagricultural periods (Refuge-Deptford and St. Catherines periods) and the two agricultural periods (Savannah and contact periods) is 2.5% on average (table 6-5). The magnitude of this difference approaches that previously observed between trophic levels (i.e., 3‰: Wada, 1980; Schoeninger and DeNiro, 1984; Schoeninger, 1985), although it is unlikely to represent a dietary change of such magnitude. It is more likely that the difference represents a decrease in use of marine foods. The difference in δ15N values obtained in a previous study (Schoeninger et al., 1983) between southwestern U.S. pueblo agriculturalists and Eskimos was 10‰ (table 6-5). This difference includes a trophic level separation of 3‰ between the more meat-dependent (carnivorous) Eskimos and the more plant-dependent (herbivorous) pueblo agriculturalists (Schoeninger and Spielmann, 1986). For comparison, the difference in δ13C values previously observed between marine and terrestrial fauna on the same trophic level is approximately 6‰ (Schoeninger and DeNiro, 1984). The difference observed in bone collagen of modern marine and terrestrial animals analyzed in this study was also 6‰ (table 6-1). Based on this line of reasoning, it is most likely that the human populations inhabiting the Georgia coast during the preagricultural and agricultural periods altered their diets to include less marine foods. The 2.5‰ shift is significant when it is considered that the largest shift expected would be 6‰.

The carbon isotope ratios become more positive through time. This is the kind of pattern which would be produced if maize is replacing marine foods and previously exploited C3 plants and animals feeding on C3 plants (i.e., deer).

PREAGRICULTURAL DIETS: Figure 6-3 shows the preagricultural samples compared with a sample of Eskimo marine hunter/fishers (Schoeninger et al., 1983). The Refuge-Deptford period sample displays a range of δ13C values which overlaps the range observed for the Eskimo, strengthening the conclusion that there was significant use of marine foods by at least some individuals within this preagricultural period. Interestingly, there are two individuals within the sample who have δ13C values (−18.6 and −17.0‰) indicative of a significant use of terrestrial foods. An individual eating only terrestrial C3-based food (acorn, hickory, deer, rabbit, and etc.) should have a bone collagen δ13C value of around −21‰ (as observed in the deer in table 6-1). Thus, within the sample from the Refuge-Deptford period, there are individuals who had different lifelong dietary adaptations.

The δ13C values for the sample from the preagricultural St. Catherines period fall near the center of the distribution for the Eskimo sample (fig. 6-3). None of the individuals from the St. Catherines period have δ13C that are as negative as observed in the earlier period. This further supports the suggestion of a more focused dietary adaptation with less dependence on C3 plants and animals feeding on C3 plants. The nitrogen values, however, are about the same and are, on average, 5‰ less positive than those in the Eskimo sample. In part, this reflects a trophic level separation between carnivorous Eskimos and omnivorous coastal Georgians.

It would appear, then, that some food item enriched in 13C (but with similar nitrogen values) was being used by some individuals during the Refuge-Deptford period and by all individuals analyzed during the St. Catherines period. Two possibilities present themselves. First, maize or some other C4 plant (enriched in 13C but not in 15N) may have been eaten. Because maize has a low protein content, it would contribute little of the nitrogen which is incorporated into bone collagen and thus would not affect the δ15N value of collagen (see discussion in Schoeninger, 1989). Admittedly, there is no archaeological evidence in support of this possibility. Ex-
amination of St. Catherines period dentitions from St. Catherines Island (Johns Mound, Marys Mound) shows very few carious lesions, which has been interpreted as indicating little or no consumption of maize (Larsen and Thomas, 1982). No botanical remains of maize have been found in the St. Catherines period or earlier sites. Nevertheless, it is worth noting that:

\[ \ldots \text{the fact that the remains of corn have not been found in pre-Savannah period contexts does not preclude the existence of corn as a dietary foodstuff in earlier periods because, as is obvious, the sample of ethnobotanical remains is quite limited (Larsen, 1982: 166).} \]

Second, increased use of a marine food from a low trophic level might be able to produce the same pattern of enriched $^{13}$C without enriched $^{15}$N. It is unlikely that seaweed, near the base of the trophic system, became a significant food, but an increased dependence on molluscs might result in the observed pattern. Preliminary results from a study of molluscs used by the prehistoric inhabitants of Nantucket Island off the coast of Massachusetts indicate that mollusc $^{15}$N values fall at the more negative end of the distribution of marine animals ($+6$ to $+10\%$) (Medaglia et al., 1989). The $^{13}$C values from the same study span a range of $-20$ to $-14\%$. If molluscs with the more positive values ($-14\%$) were being eaten selectively, then at least 50% of the carbon in each person's skeleton would have had to come from molluscs. Given our present knowledge of metabolism, this would

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**Fig. 6-2.** $\delta^{15}$N and $\delta^{13}$C values for the preagricultural sample (Refuge-Deptford and St. Catherines periods) and the agricultural sample (Savannah and contact periods). Between the two archaeologically identified adaptations, there is a decrease in nitrogen delta values and an increase in carbon delta values. The trend indicates a decrease in use of marine foods coupled with increasing dependence on maize (compare with fig. 6-1).
**Fig. 6-3.** $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the two samples from the preagricultural periods (Refuge-Deptford and St. Catherines) compared with the values from a sample of Eskimo from a previous study (Schoeninger et al., 1983). The individuals from St. Catherines Island have $\delta^{15}\text{N}$ values that are 5% lower, on average, than the Eskimo. This reflects the use by Eskimo of animals higher in the trophic system (e.g., toothed whales) than those (molluscs and fish) used by coastal Georgians. It also reflects higher intake of meat by the Eskimo. The $\delta^{13}\text{C}$ values of all groups overlap indicating significant use of marine foods by the preagricultural inhabitants of St. Catherines Island.

mean that a minimum of 50% of these peoples’ calories would have come from molluscs. Such a solution requires an overall decrease in the proportion of calories obtained from plants.

At this point, it is not possible to draw definitive conclusions. It is important to note, however, that molluscs were harvested on the coast during the winter months at a time when their carbohydrate levels were high relative to protein (Claassen, 1986a). This might serve to alleviate the difficulty of obtaining sufficient calories from molluscs. If, however, the molluscs chosen for food had $\delta^{13}\text{C}$ values near the $-20\%\text{o}$ end of the range, nearly 100% of calories would have had to come from the molluscs.

**Agricultural Diets:** A marked difference in both carbon and nitrogen is obvious in the Savannah period relative to the preagricultural periods (tables 6-4 and 6-5). Figure 6-4 shows that the nitrogen isotope values have dropped so that the distribution now overlaps that of a previously analyzed sample of pueblo agriculturalists (Schoeninger et al., 1983). The bulk of the data falls within the range of $+9.5$ to $+11.5\%\text{o}$ which is slightly higher than that of the pueblo group, reflecting continued use of marine foods. Further, there is one individual with a $\delta^{15}\text{N}$ value of
Fig. 6-4. $\delta^{15}$N and $\delta^{13}$C values of the sample of precontact agriculturalists from the Georgia coast (Savannah period) and the contact period agriculturalists from St. Catherines Island compared with a sample of Pueblo agriculturalists from a previous study (Schoeninger et al., 1983). The more positive carbon and nitrogen isotope ratios in the coastal sample reflects continued use of marine foods although the carbon values are too positive to be due to marine foods alone. Only the inclusion of a C4 plant, such as maize, can account for such enriched values.

$+13.3\%$, indicating that at least some of the individuals from this time period continued to include an amount of marine food similar to previous periods. In other words, the range of values overall indicates a continued varied range of diet items although a shift toward dependence on terrestrial sources appears obvious.

The carbon delta values also encompass a fairly large range (6%). The average value, however, has shifted from that of the preceding period in the direction expected from an increased inclusion of maize in diet. When compared with the pueblo agriculturalists, however, it is obvious that the precontact maize agriculturalists of the Georgia coast were not using maize to the same extent. Some marine foods continued to be important, although only a C4 plant like maize can account for the relatively positive carbon signature and low value of the nitrogen signature observed in these samples. The precontact agricultural Savannah period represents a time span on the order of the St. Catherines period (150 years), yet the range of individual diets is much greater in the Savannah period. This is probably due to differential acceptance of maize as a new economic endeavor and as a diet item.

The average $\delta^{13}$C value for the sample from the contact period is $-11.5\%$. This value is over 3% less positive than the average for
the pueblo sample. This indicates less dependence on corn by the island inhabitants, although the magnitude of the difference cannot be assessed at present. Samples of maize kernels recovered from Santa Catalina have a $\delta^{13}C$ value of around $-12\%$ (table 6-4) which is the value most often reported for this C4 plant. In the absence of all marine foods, a bone collagen $\delta^{13}C$ value of around $-8\%$ (as seen in the pueblo sample) would be expected for a diet in which the carbohydrate staple is maize. The observed value of $-11.5\%$ suggests a significant contribution from maize, while the slightly elevated nitrogen values suggest continued use of marine foods. The large range of carbon isotope values compared with that in the pueblo sample indicates that a greater range of food categories were used by individuals living in the mission.

Compared with the precontact agricultural Savannah period, the contact period population appears to have been depending to a greater extent on maize. This is suggested by the lower $\delta^{15}N$ and higher $\delta^{13}C$ value and by the difference in distribution of the values for the two samples. The bulk of the sample from the contact period displays isotope values indicative of lower dependence on marine foods and greater dependence on maize.

**CONCLUSIONS**

The overall pattern of change in human dietary adaptation is that of decreasing use of marine foods (particularly molluscs and fish) and increasing use of maize. The data from the earliest period (Refuge-Deptford: 1100 B.C.-A.D. 500) are more scattered than would be expected for a single dietary regime. The individuals analyzed probably enjoyed diets that ranged from less than 30 percent of calories from marine foods to over 50 percent from marine sources. This fits well with Larsen’s (1982) assessment of the lifeway during this period as being mobile, providing the inhabitants with the opportunity to extract foods from several environments. At certain times during the period, parts of this population subsisted to a great extent on terrestrial food supplies. These may have been the times of lower sea levels when molluscs and marshland fish would not have been in plentiful supply. At other times, the population included a large quantity of marine foods in diet.

There appears to be an increase in the carbon isotope ratio, on average, in the preagricultural St. Catherines period (A.D. 1000–1150) as compared with the earlier Refuge-Deptford period. This increase is coupled with a stable nitrogen isotope ratio similar to that documented in the earlier period. This pattern could be produced by adding maize to the diet, although there is as yet no archaeological evidence for the presence of maize in this period. It is possible that increasing dependence on a marine food low in the trophic pyramid could also produce this pattern. Reitz (1985) suggested that oysters became more important as a diet component during the St. Catherines period; and Claassen (1986a) noted that they were collected in a season in which they had the highest carbohydrate concentration in the yearly cycle. Such a solution would require that molluscs provide 50–100 percent of total dietary calories. Neither alternative (maize nor molluscs) can be strongly supported at this time.

The nitrogen stable isotope ratios indicate that a marked decrease in use of marine products occurred around the time of the Savannah period (A.D. 1150–1300), the period with the earliest archaeological evidence for use of maize. The large range in carbon stable isotope ratios from the sample dating to this period indicates that there was differential dependence on maize within the population. Even so, the majority of individuals within the sample have carbon stable isotope ratios that are too enriched in $^{13}C$ to be explained by dependence on marine foods. This is true especially when the relatively low nitrogen isotope ratio is considered.

The data for the contact period indicate a diet in which a greater percentage of calories is derived from maize, but in which a significant proportion of the protein is marine in origin. This pattern agrees with the archaeological evidence for diet and also with written records concerning the life of the aboriginal populations within the mission system (see Larsen, this volume). Such an increased dependence on maize coupled with the restriction in variety of alternative food items may account for some of the patholo-
gies noted elsewhere in this volume in the contact period. The combination of stresses produced by infectious disease, marginal nutrition, demands by the Spanish overlords, and life in settled, perhaps crowded, communities may have contributed to the eventual extinction of these populations.

ACKNOWLEDGMENTS

We thank Mr. John Bernitz (Northeastern University), Mr. Bruno Marino, Mr. Matthew Murray, and Mr. John Ritch (all of Harvard University), and Mr. John Lanham and Ms. Debbie Alder (both of University of Cape Town) for their help in the preparation and analysis of samples. This study was funded by grants from the National Science Foundation (grant BNS-8406773) and the Foundation for Research Development of the Council for Scientific and Industrial Research, Republic of South Africa.
CHAPTER 7. POSTCRANIAL BIOMECHANICAL ADAPTATIONS TO SUBSISTENCE STRATEGY CHANGES ON THE GEORGIA COAST

CHRISTOPHER B. RUFF AND CLARK SPENCER LARSEN

ABSTRACT

Temporal changes in structural strength of the femur and humerus in Georgia coastal populations were evaluated by measuring bone geometric section properties (cross-sectional areas and second moments of area). Three locations were examined through sectioning and direct measurement: mid-distal humerus (35% of bone length from the distal end), midshaft femur (50% from distal end), and subtrochanteric femur (80% from distal end). The samples were divided into three temporal subsamples—precontact preagricultural, precontact agricultural, and contact. Cross-sectional properties were standardized over powers of bone length to allow for comparisons of relative strength in the different temporal periods.

We reported elsewhere (Ruff et al., 1984) that relative structural strength of the femur declines between the precontact preagricultural and agricultural periods in both females and males. Our findings in the present investigation indicate that this trend is reversed in the contact period, where femoral strength increases, more so in females than in males. The trend of an initial decrease followed by an increase in strength is also characteristic of male humeri over the three periods. Female humeri also show a decrease in relative strength in the precontact agricultural period, but then show no reversal, and continue to decrease in strength in the contact period. General body size decreases and sexual dimorphism in body size increases in the precontact agricultural period. These trends again reverse in the contact period.

These results indicate that the pattern of decreased postcranial skeletal robusticity previously observed in the transition from hunting and gathering to a lifestyle based at least in part on maize agriculture is not continued in the contact period, except in the female upper limb. The behavioral implications of these findings are discussed.

INTRODUCTION: MECHANICAL MODELS

Studies of postcranial skeletal adaptation to changes in subsistence strategy have most commonly concentrated on changes in whole body size (stature), occasionally also including general body proportions and overall robusticity (e.g., see references in Larsen, 1982: 184; and reports in Cohen and Armelagos, 1984). This emphasis may stem partly from an overriding concern with the direct dietary effects on the skeleton of a subsistence strategy change; that is, the impact of nutritional factors on skeletal growth and development (e.g., Guzman, 1968). However, other indirect effects of change in subsistence technology may also have a major bearing on both skeletal size and shape characteristics. In particular, behavioral changes accompanying such an environmental shift may have a large effect on the mechanical forces applied to the skeleton throughout life, leading to adaptive bone remodeling in response. Attempts to interpret differences in bone structure in terms of mechanical factors, then, may lead to a more complete understanding of the biobehavioral changes which occurred concomitant with a change in subsistence strategy.

The diaphyseal shape of long bones is one structural characteristic which has been overlooked or deemphasized in most recent studies of skeletal environmental adaptation. This is true despite the fact that systematic changes through the Holocene in diaphyseal shape have long been recognized (Buxton, 1938; Lovejoy, 1970; Brothwell, 1972), as has the fact that bones remodel in response to changes in applied mechanical loads (Wolff, 1892; Liskova and Hert, 1971; Goodship et al., 1979; Woo et al., 1981), albeit through a mechanism which is still unclear (e.g., Lyon, 1986). One reason for this relative neglect is that changes in diaphyseal form may be subtle and difficult to measure using traditional osteometric techniques (Martin, 1928), and there is large apparent individual variation in overall shape which has proved difficult to interpret in relation to consistent patterns (e.g., Hrdlička, 1934). However, using biomechanical beam theory first devel-
oped by mechanical and civil engineers (Timoshenko and Gere, 1972), it is possible to reduce complex cross-sectional shapes of long bones to several critical properties which can be interpreted in a relatively straightforward mechanical sense. Because differences in mechanical loadings at least partly reflect differences in behavior, results of these analyses can be used to help reconstruct past behavioral characteristics of the population samples under study.

Although the general approach of using mechanical beam theory to analyze long bone structure was used over 70 years ago by Koch (1917), it was not until the late 1960s and through the 1970s that this technique was applied to samples larger than one bone (Klennerman et al., 1967; Ammann, 1971; Kimura, 1971, 1974; Minns et al., 1975; Lovejoy et al., 1976; Piziali et al., 1976; Martin and Atkinson, 1977; Miller and Piotrowski, 1977; Jungers and Minns, 1979). Even these studies, however, were limited to small samples—in most cases 10 or fewer individuals—by the tediousness of the manual calculations involved in determining the necessary parameters. With the development of more automated techniques of measurement (e.g., Nagurka and Hayes, 1980), it has become possible to carry out truly large-scale demographic studies of variation in cross-sectional structural characteristics within and between populations (Ruff and Hayes, 1983a, 1983b, 1984; Ruff et al., 1984; Sumner, 1984; Bridges, 1985, 1989; Brock, 1985; Brock and Ruff, 1988; Van Gerven et al., 1985; Ruff, 1987). These studies have addressed a variety of long-standing anthropological issues using biomechanics theory, including behavioral changes associated with shifts in subsistence strategy, the relationship of sex differences in activity patterns to subsistence technology, and alterations in skeletal growth and development in response to environmental (including nutritional) changes.

In a mechanical beam model, the rigidity, or strength of a long bone is determined by two types of properties: area and second moments of area of bone tissue in a cross section through the diaphysis. The cross-sectional area is proportional to strength in compression and tension applied nonecentrically (that is, not off the central longitudinal axis of the diaphysis), and second moments of area, also referred to as moments of inertia, are proportional to strength in bending and torsion (twisting) of the shaft. Because (1) most mechanical loadings are applied eccentrically due to bone curvature and the off-center position of muscle insertions and other related factors, (2) bone tissue is weaker in tension and shear than in compression, and (3) tension and shear will almost always be the result of bending and torsion, second moments of area are generally more critical than area in evaluating bone mechanical function. Second moments of area used in bending strength analyses are calculated about an axis running through the bone cross section and are generally denoted "Iₓ," with "x" referring to the axis about which the property is calculated, while the analogous property used in torsional analyses is denoted "Jₓ," the polar second moment of area, and is calculated about the center of the section (details can be found in the references cited above). Different long bone cross sections along the length of a shaft may be characterized by different combinations of area, I's in different planes, and J, depending upon what particular combination of mechanical forces it is designed to withstand (see Ruff and Hayes, 1983a). J also happens to be equal to the sum of any two I's measured in perpendicular planes, and so can be used as a measure of (twice) average bending strength in all planes. This kind of analysis assumes that geometric rather than material properties of bones (i.e., density, elasticity) are most important as indicators of mechanical function; this assumption is supported by experimental in vivo studies of altered mechanical loadings and their effects on bone structure (e.g., Woo et al., 1981).

One simple example will suffice to illustrate the altered perspective on bone structural adaptation which a biomechanical approach can provide. Percent cortical area (PCCA), or percent cortical thickness (PCCT) as it is sometimes calculated, is a measure of compact cortical bone relative to subperiosteal area or breadth which can be measured or estimated from radiographs (e.g., Garn, 1970). This index has been widely used as a health indicator in archaeological samples, with lower indices generally interpreted to mean a decline in nutritional status (e.g., D.
Cook, 1984; Brown, 1988), implying some kind of "negative" effect on bone structure. However, neither index has any relevance to the structural strength or function of a bone, and a lower index may even be associated with an increase in strength. For example, consider two circular long bone cross sections, the first with an outer diameter of 20 mm and an inner diameter of 10 mm, the second with an outer diameter of 25 mm and an inner diameter of 17 mm (fig. 7-1). In the second section, cortical thickness has declined 20 percent and PCCT and PCCA have declined by about a third. However, due to the relatively outward redistribution of bone (subperiosteal and endosteal expansion), cortical area in the second section actually increases by 12 percent and second moments of area about double. Thus, what might have been interpreted as a "decline" in nutritional status may actually indicate an increase in mechanical loadings (through activity or other changes) This particular fallacy has been noted with respect to adult skeletal aging trends (in osteoporosis) (Ruff, 1981: 239), as well as childhood growth and development (Van Gerven et al., 1985).

It should be emphasized that obtaining complete two-dimensional cross sections and using relatively complex algorithms to calculate geometric properties (Nagurka and Hayes, 1980) are not as important in this respect as the general approach (also see Ruff, 1987). Second moments of area can be estimated from radiographic measurements using simple formulas (e.g., Klenerman et al., 1967; Fresia et al., this volume), and the general engineering principles underlying the technique have now appeared in several anthropological reports, as noted above. The present study and the following chapter by Fresia and co-workers illustrate the ongoing use of this method in the analysis of skeletal material from the Georgia coast region.

PREVIOUS WORK

We have previously reported on changes in bone structure of the femur which occurred from precontact preagricultural to precontact agricultural periods on the Georgia coast (Larsen, 1982; Ruff et al., 1984). We showed that with the transition to agriculture, femora became not only shorter in length, but also relatively weaker, even for a smaller body size. This reduction in strength was brought about by a contraction of bone tissue toward the medullary cavity, and not a change in total bone volume or mass relative to length. Furthermore, there was an increase in diaphyseal circularity with the transition, indicating less well-defined patterns of mechanical loading, or applied forces. We concluded that the agricultural sample was characterized by a relative decrease in mechanical loadings of the lower limb, in addition to any changes in overall body size brought about by a combination of dietary and behavioral factors. The decrease in mechanical loadings was about equal for males and females, although other evidence indicated that a reduction in nutritional quality per se may have been greater among females. There was also some indication that types of mechanical loadings, i.e., forces applied in different planes of the lower limb, may have changed to some degree between periods, especially among males.

In the present study, we have extended the investigation to include the major upper limb bone—the humerus. We also now include both humeri and femora from the contact period on the Georgia coast. Thus, we can
now examine changes in both upper and lower limbs, as well as the effects of the new environmental changes occurring after the arrival of Europeans.

MATERIALS AND METHODS

A total of 62 femora and 80 humeri from the Georgia coast were included in the study (table 7-1). Each sample is approximately evenly divided between adult males and females, right and left sides, and precontact preagricultural, precontact agricultural, and contact temporal periods. Only one humerus or femur or both was studied for each individual, with about 60 percent of the upper and lower limb bones matched (i.e., from the same individual). Sex was determined primarily on the basis of pelvic morphology as well as other indicators (Larsen, 1982; Larsen, unpubl. data), and age was estimated primarily on the basis of functional dental wear (Larsen, 1982; Russell et al., this volume). The provenience of the precontact samples has been described previously (Larsen, 1982; Ruff et al., 1984; see also table 7-1). The contact sample was derived principally from the mission cemetery of Santa Catalina de Guale, although several specimens were also included from other contact period sites at the nearby Pine Harbor site and Mission Santa Catalina de Guale de Santa Maria on Amelia Island (F. Cook, 1980; Larson, 1980; Hardin, 1986; Larsen and Saunders, 1987; see also table 7-1). Only complete specimens with intact ends and relatively unweathered subperiosteal surfaces were used in the study. This largely explains the much smaller number of individuals available for analysis than were included in overall demographic studies for these samples (Larsen, 1982; Russell et al., this volume).

Each bone was first oriented in standardized anteroposterior (A-P) and mediolateral (M-L) planes and locations of cross sections to be analyzed were determined. For the femur, anatomical orientation and measurement of length’ (used in locating sections) followed that described in Ruff and Hayes (1983a). (Note that length’ refers to the distance from the distal surfaces of the condyles to the superior edge of the femoral neck, and thus does not include the femoral head.) Two

<table>
<thead>
<tr>
<th>TABLE 7-1 Sample Composition</th>
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</thead>
<tbody>
<tr>
<td></td>
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<tr>
<td></td>
</tr>
<tr>
<td>Temporal period/site*</td>
</tr>
<tr>
<td>Precontact preagricultural</td>
</tr>
<tr>
<td>Sea Island Mound</td>
</tr>
<tr>
<td>Johns Mound</td>
</tr>
<tr>
<td>Marys Mound</td>
</tr>
<tr>
<td>McLeod Mound</td>
</tr>
<tr>
<td>Deptford</td>
</tr>
<tr>
<td>Airport</td>
</tr>
<tr>
<td>Cannons Point</td>
</tr>
<tr>
<td>Charlie King Mound</td>
</tr>
<tr>
<td>Total</td>
</tr>
<tr>
<td>Precontact agricultural</td>
</tr>
<tr>
<td>Irene Mound</td>
</tr>
<tr>
<td>Total</td>
</tr>
<tr>
<td>Contact</td>
</tr>
<tr>
<td>Santa Catalina de Guale</td>
</tr>
<tr>
<td>(St. Catherines Island)</td>
</tr>
<tr>
<td>Santa Catalina de Guale</td>
</tr>
<tr>
<td>(Amelia Island)</td>
</tr>
<tr>
<td>Pine Harbor</td>
</tr>
<tr>
<td>Total</td>
</tr>
<tr>
<td>Grand total</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

* A discussion of the precontact sites is presented in Larsen (1982) and Ruff et al. (1984). Provenience for the contact sites is presented in Larsen (this volume), Saunders (1987), and F. Cook (1980).

cross sections were included—at 50 percent (midshaft) and at 80 percent (subtrochanteric) of length’ measured from the distal end of the bone (fig. 7-2).

For the humerus, the following orientation was used: the coronal (M-L) plane is defined by the mediolateral articular axis of the capitulum and trochlea and the anteroposterior midpoint of the diaphysis at the level of the surgical neck; the sagittal (A-P) plane is perpendicular to the coronal plane and intersects the M-L midpoint of the surgical neck and the lateral lip of the trochlea parallel to the longitudinal axis of the shaft. One cross section at 35 percent of bone length’ measured from the distal end was included (fig. 7-2). (Length’ is the length of the humerus from the proximal surface of the humeral head to the distal edge of the lateral lip of the trochlea.) This location was chosen for analysis
because it avoids the flexor and extensor ridges and the deltoid tuberosity, and thus should minimize the effects of localized stresses due to muscle insertions. It is also convenient for radiographic measurement (e.g., Fresia et al., this volume) and has been used in the past as a site of measurement for humeral structural analyses (Bloom and Laws, 1970; Ruff and Jones, 1981).

After preorientation and identification of section locations, bones were sectioned transversely using a fine-toothed band saw at each location. Section surfaces were photographed and rear-projected onto a digitizer screen, and subperiosteal and endosteal boundaries traced (Ruff and Hayes, 1983a). Point coordinates were input to program SLICE, which calculates geometric section properties (Nagurka and Hayes, 1980). These include cortical area (CA), medullary area (MA), total subperios-

Fig. 7-2. Locations of femoral (top) and humeral (bottom) sections included in the study. See text and Ruff and Hayes (1983a) for description of length’ measurement.
teal area (TA), maximum and minimum second moments of area (I_max and I_min, respectively), second moments of area about x (mediolateral) and y (anteroposterior) axes (I_x and I_y, respectively), and polar second moment of area (J). The mechanical interpretation of these properties has been discussed above.

Although approximately equal numbers of right and left sides were included in each sex/temporal period grouping, the inclusion of both sides in the analysis will increase the sample variances due to bilateral asymmetry, especially in the upper limb (Fresia et al., this volume). Therefore, prior to statistical comparisons, “side adjusted” values for all humeral geometric properties were calculated based on radiographic estimates of bilateral asymmetry (Fresia et al., this volume). Percentage differences between right and left sides for all properties were calculated for all individuals in the radiographic study (N = 49). The directly measured geometric properties used in the present study were then adjusted upward or downward by this factor depending on the direction of asymmetry and whether the sectioned bone was from the left or right side. The same procedure was carried out for those individuals not included in the radiographic study using the mean bilateral asymmetry values for that sex and temporal period. In effect, this establishes “average humerus” properties for each individual and should eliminate the effect of side differences in the analysis. No similar procedure was performed for femora, because bilateral asymmetry is much less marked in the lower limb (Ruff and Jones, 1981).

Because there are length (“size”) differences between the samples analyzed (Larsen, 1982; Ruff et al., 1984; also see below), cross-sectional data were analyzed both before and after standardizing for “size” variation. For size-standardized analyses, all cross-sectional areas were divided by bone length^2 and second moments of area by bone length^4 (Ruff, 1984).

Statistical evaluation of sex and temporal period differences was carried out using two-way analysis of variance (sex, period), one-way ANOVA within sexes (period), and t-tests between temporal periods within sexes. Differences were considered statistically significant at the p < 0.05 level, and near-significant between p < 0.05 and p < 0.10.

RESULTS

TEMPORAL TRENDS: WHOLE BONE DIMENSIONS AND AGE: Temporal differences in bone length of the femur and humerus and two angular measurements of the femur are presented in table 7-2. Average ages of the samples, by sex, are also listed. Bone lengths include both maximum length and length’, as defined in Ruff and Hayes (1983a) and above. The cervicodiaphyseal and antetorsion angles of the femur are measures of the relative angulation of the femoral head and neck in the frontal and transverse planes, respectively, and are also defined in Ruff and Hayes (1983a).

In table 7-2 and in subsequent tables, means and standard errors are shown by sex and the three temporal periods (precontact preagricultural, precontact agricultural, and contact), along with the mean differences between each pair of temporal periods and the results of the one-way ANOVAs carried out over the three periods within sex. Results of the two-way ANOVAs for all properties are given in table 7-9.

As shown in table 7-2, femoral bone length shows significant temporal variation in females. Females first decline in length from the precontact preagricultural to the precontact agricultural periods, then increase again in the contact period, although not to as great a length as in the precontact preagricultural period. Female humeri show the same general temporal trends, although the differences (except precontact agricultural to contact) are not significant. Male femora exhibit similar, but smaller variation in length between periods, with no differences reaching significance. Male humeri show very little temporal variation in length, with precontact agricultural and contact humeri essentially identical in length on average. Temporal trends in bone length are illustrated graphically in figures 7-3 and 7-4.

Antetorsion of the femur also shows significant temporal variation in both sexes. Precontact preagricultural and precontact agricultural femora have relatively high angles, with a significant increase between the pe-
### TABLE 7-2
Temporal Differences in Whole Bone Dimensions and Age

<table>
<thead>
<tr>
<th>Property(^a)</th>
<th>Preag. Mean</th>
<th>SE</th>
<th>Agric. Mean</th>
<th>SE</th>
<th>Contact Mean</th>
<th>SE</th>
<th>Group differences</th>
<th>1-Way ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male femora</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. In.</td>
<td>450.9</td>
<td>7.9</td>
<td>437.4</td>
<td>3.6</td>
<td>449.2</td>
<td>6.9</td>
<td>-13.5(^b)</td>
<td>11.8</td>
</tr>
<tr>
<td>Length'</td>
<td>424.9</td>
<td>7.9</td>
<td>411.2</td>
<td>3.7</td>
<td>421.5</td>
<td>6.4</td>
<td>-13.7(^b)</td>
<td>10.3</td>
</tr>
<tr>
<td>CD ang.</td>
<td>131.0</td>
<td>1.5</td>
<td>129.8</td>
<td>1.1</td>
<td>129.7</td>
<td>2.1</td>
<td>-1.2</td>
<td>-0.1</td>
</tr>
<tr>
<td>Ant. ang.</td>
<td>23.2</td>
<td>2.2</td>
<td>23.6</td>
<td>2.0</td>
<td>14.8</td>
<td>2.3</td>
<td>0.4</td>
<td>-8.4(^c)</td>
</tr>
<tr>
<td>Age</td>
<td>25.5</td>
<td>1.4</td>
<td>23.8</td>
<td>1.3</td>
<td>32.5</td>
<td>2.1</td>
<td>-1.7</td>
<td>9.7(^c)</td>
</tr>
<tr>
<td>Female femora</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. In.</td>
<td>440.2</td>
<td>6.5</td>
<td>400.3</td>
<td>5.2</td>
<td>430.6</td>
<td>6.4</td>
<td>-39.9(^c)</td>
<td>30.3(^d)</td>
</tr>
<tr>
<td>Length'</td>
<td>415.2</td>
<td>6.0</td>
<td>376.4</td>
<td>5.0</td>
<td>401.2</td>
<td>5.6</td>
<td>-38.8(^c)</td>
<td>24.8(^d)</td>
</tr>
<tr>
<td>CD ang.</td>
<td>129.8</td>
<td>0.9</td>
<td>133.4</td>
<td>1.7</td>
<td>129.4</td>
<td>1.3</td>
<td>3.6(^b)</td>
<td>-4.0</td>
</tr>
<tr>
<td>Ant. ang.</td>
<td>23.2</td>
<td>2.7</td>
<td>31.9</td>
<td>2.9</td>
<td>16.8</td>
<td>2.0</td>
<td>8.7(^c)</td>
<td>-15.1(^c)</td>
</tr>
<tr>
<td>Age</td>
<td>30.3</td>
<td>3.2</td>
<td>26.1</td>
<td>1.5</td>
<td>35.9</td>
<td>2.6</td>
<td>-4.2</td>
<td>9.8(^d)</td>
</tr>
<tr>
<td>Male humeri</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. In.</td>
<td>322.6</td>
<td>5.3</td>
<td>317.5</td>
<td>2.7</td>
<td>317.2</td>
<td>3.6</td>
<td>-5.1</td>
<td>-0.3</td>
</tr>
<tr>
<td>Length'</td>
<td>318.3</td>
<td>5.1</td>
<td>312.5</td>
<td>2.6</td>
<td>313.2</td>
<td>3.5</td>
<td>-5.8</td>
<td>0.7</td>
</tr>
<tr>
<td>Age</td>
<td>29.6</td>
<td>2.3</td>
<td>26.8</td>
<td>1.8</td>
<td>31.9</td>
<td>2.0</td>
<td>-2.8</td>
<td>5.1</td>
</tr>
<tr>
<td>Female humeri</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max. In.</td>
<td>308.9</td>
<td>7.9</td>
<td>294.1</td>
<td>2.9</td>
<td>305.5</td>
<td>4.7</td>
<td>-14.8(^c)</td>
<td>11.4(^c)</td>
</tr>
<tr>
<td>Length'</td>
<td>305.8</td>
<td>7.8</td>
<td>290.2</td>
<td>2.8</td>
<td>302.2</td>
<td>4.7</td>
<td>-15.6(^b)</td>
<td>12.0(^c)</td>
</tr>
<tr>
<td>Age</td>
<td>29.8</td>
<td>3.6</td>
<td>29.0</td>
<td>1.8</td>
<td>37.0</td>
<td>2.5</td>
<td>-0.8</td>
<td>8.0(^c)</td>
</tr>
</tbody>
</table>

\(^a\) Properties are maximum length (Max. In.), length used in determining cross-section locations (Length'), cervicodiaphyseal angle (CD ang.), and antetorsion angle (Ant. ang.). Lengths are in mm, angles in degrees, age in years.

Significance levels for \(t\)-tests between groups and 1-Way ANOVA between groups within sex:

\(^b\) \(p < 0.10\);

\(^c\) \(p < 0.05\);

\(^d\) \(p < 0.01\);

\(^e\) \(p < 0.001\).

...
and contact periods, which may be partly related to the older average age of the contact sample (table 7-2), because PCCA declines with age (Garn, 1970; Ruff, 1981). PCCA also increases in the male subtrochanteric section between the precontact preagricultural and precontact agricultural periods, which again may be partly related to the lower average age of males in the precontact agricultural period.

The ratios $I_{\text{max}}/I_{\text{min}}$ and $I_x/I_y$ are cross-sectional “shape” indices which reflect the relative distribution of bone in perpendicular planes (Ruff and Hayes, 1983a; Ruff, 1987). $I_{\text{max}}/I_{\text{min}}$ measures maximum to minimum bending strength, and $I_x/I_y$ measures relative anteroposterior to mediolateral bending strength. Because the orientation of the subtrochanteric section makes interpretation of $I_x/I_y$ difficult (e.g., see Ruff and Hayes, 1983a: fig. 7-6), only $I_{\text{max}}/I_{\text{min}}$ is given for this section. The only statistically significant change in these ratios in the midshaft section is a decline in $I_x/I_y$ in males between the precontact preagricultural and precontact agricultural periods, although there is also a near significant decline in this index in females between precontact preagricultural and contact periods. In general, females decline in this index through time, while males first decline, then increase. In the subtrochanteric section, both sexes show a decline through time in $I_{\text{max}}/I_{\text{min}}$ (figures 7-5 and 7-6).

Theta measures the orientation of the major axis, or direction of greatest bending rigidity of a section, here measured counterclockwise from the lateral direction looking distally (see Ruff and Hayes, 1983a). It should be

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**Fig. 7-3.** Temporal changes in femoral length.
noted that the mean theta value for the precontact agricultural female 50 percent section has been changed from the original description of this sample (Ruff et al., 1984), due to a revision in the way in which theta ranges were determined (for details see Ruff, 1981). Among males, theta of the midshaft is significantly greater (i.e., nearer the A-P axis) in the precontact preagricultural period than in the other two periods; females show no significant trends. Variation in theta of the subtrochanteric section parallels variation in the antetorsion angel (also see Ruff, 1981), being closer to 180° (i.e., mediolateral) when the antetorsion decreases, or approaches a more mediolateral orientation (table 7-2).

Temporal changes in cross-sectional geometric properties of the femur standardized for bone length ("size") differences are shown in tables 7-5 and 7-6. Size standardized cortical area (CA) shows no temporal variation among males or among females in the first two temporal groups. However, contact females show a significant increase in size standardized CA at both midshaft and subtrochanteric sections. In terms of relative positions of the subperiosteal (TA) and endosteal (MA) surfaces (see Ruff et al., 1984), both males and females show a relative "contraction" of the femoral cortex from precontact preagricultural to precontact agricultural, leading to declines in standardized TA and MA, but not in CA. This process is then reversed in the contact period, with an increase in standardized TA and MA in both sexes. However, TA increases more than MA in females, leading to an increase in CA as well in the contact period.

The effects of these changes in cortical geometry are generally to decrease second mo-
### TABLE 7-3

Temporal Differences in Midshaft Femoral Cross-sectional Dimensions and Indices—Unstandardized

<table>
<thead>
<tr>
<th>Property</th>
<th>Preag. Mean</th>
<th>SE</th>
<th>Agric. Mean</th>
<th>SE</th>
<th>Contact Mean</th>
<th>SE</th>
<th>Group differences</th>
<th>1-Way ANOVA</th>
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<td>Ag-Pre</td>
<td>Cont-Ag</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>CA</td>
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<td>396.1</td>
<td>11.8</td>
<td>414.4</td>
<td>17.3</td>
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</tr>
<tr>
<td>MA</td>
<td>147.8</td>
<td>16.1</td>
<td>105.1</td>
<td>7.8</td>
<td>158.4</td>
<td>10.5</td>
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<td>501.2</td>
<td>15.2</td>
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<td>71.7</td>
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<td>1.28</td>
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<td>1.08</td>
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<td>61.2</td>
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<td>10.0</td>
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<td><strong>Females</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CA</td>
<td>326.2</td>
<td>16.2</td>
<td>264.2</td>
<td>12.6</td>
<td>337.9</td>
<td>10.6</td>
<td>-62.0</td>
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<td>49.0</td>
<td>10.5</td>
<td>30.4</td>
<td>-40.4</td>
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</table>

* CA = cortical area; MA = medullary area; TA = total subperiosteal area; I<sub>max</sub>, I<sub>min</sub> = maximum and minimum second moments of area (S.M.A.); I<sub>L</sub>, I<sub>E</sub> = S.M.A.'s about x and y axes (A-P and M-L bending strengths, respectively); J = polar S.M.A.; PCCA = (CA/TA) \times 100; Theta = orientation of greatest bending strength. Areas in mm\(^2\), second moments of area in mm\(^4\), angle in degrees.

Significance levels for \(t\)-tests between groups and 1-Way ANOVA between groups within sex:

\* \(p < 0.10\);
\* \(p < 0.05\);
\* \(p < 0.01\);
\* \(p < 0.001\).

\(d\)
<table>
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<tr>
<th>Property&lt;sup&gt;a&lt;/sup&gt;</th>
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<th>Agric. Mean</th>
<th>SE</th>
<th>Contact Mean</th>
<th>SE</th>
<th>Group differences</th>
<th>1-Way ANOVA</th>
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</tr>
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<td></td>
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<td></td>
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<td>1.7</td>
<td>67.1</td>
<td>14.8</td>
<td>7.9&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-5.6&lt;sup&gt;e&lt;/sup&gt;</td>
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<tr>
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<td>-0.27&lt;sup&gt;e&lt;/sup&gt;</td>
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<td>148.5</td>
<td>2.7</td>
<td>6.0</td>
<td>5.1</td>
</tr>
</tbody>
</table>

| **Females**     |             |    |             |    |              |    |                  |             |
|                 |             |    |             |    |              |    |                  |             |
| CA              | 328.1       | 16.2| 269.9       | 9.8 | 348.7        | 12.9| -58.2<sup>c</sup> | 78.8<sup>c</sup> | 20.6           | <sup>d</sup> |
| MA              | 209.4       | 24.1| 125.2       | 8.0 | 160.2        | 13.0| -84.2<sup>d</sup> | 35.0<sup>d</sup> | -49.2<sup>d</sup> | <sup>d</sup> |
| TA              | 537.5       | 17.0| 395.1       | 13.7| 508.9        | 21.8| -142.4<sup>e</sup> | 113.8<sup>e</sup> | -28.6           | <sup>e</sup> |
| I<sub>max</sub> | 28,153      | 1687| 16,405      | 1171| 25,003       | 2245| -11,748<sup>e</sup> | 8598<sup>e</sup> | -3150          | <sup>e</sup> |
| I<sub>min</sub> | 13,281      | 769 | 7883        | 566 | 14,212       | 1032| -5398<sup>e</sup>  | 6329<sup>e</sup> | 931            | <sup>e</sup> |
| J               | 41,434      | 2334| 24,287      | 1648| 39,215       | 3156| -17,147<sup>e</sup> | 14,928<sup>e</sup> | -2219          | <sup>e</sup> |
| PCCA            | 61.7        | 3.5 | 68.4        | 1.4 | 69.0         | 1.9 | 6.7              | 0.6          | 7.3<sup>b</sup>  | <sup>b</sup> |
| I<sub>max</sub>/I<sub>min</sub> | 2.14 | 0.09 | 2.10 | 0.10 | 1.75        | 0.08| -0.04           | -0.35<sup>d</sup> | -0.39<sup>d</sup> | <sup>d</sup> |
| Theta           | 143.2       | 3.1 | 131.4       | 3.6 | 144.5        | 4.2 | -11.8<sup>c</sup> | 13.1<sup>c</sup> | 1.3            | <sup>c</sup> |

<sup>a</sup> Properties as in table 7-3.

Significance levels for t-tests between groups and 1-Way ANOVA between groups within sex:

<sup>b</sup> p < 0.10;
<sup>c</sup> p < 0.05;
<sup>d</sup> p < 0.01;
<sup>e</sup> p < 0.001.
ments of area in the precontact agricultural period, then increase them in the contact period. In males, these temporal trends are only significant in the subtrochanteric section, while females show significant changes at both locations. In general, females show more of an increase from precontact agricultural to contact in second moments of area than males. Temporal trends in length-standardized CA and J of the femoral midshaft are illustrated in figures 7-7 and 7-8.

In sum, whether analyzed as raw data or standardized over powers of bone length, the precontact preagricultural and contact period femora from both sexes are relatively similar in terms of overall mechanical strength, while precontact agricultural femora are relatively weaker. However, this is not necessarily true with respect to bone "shape" ratios ($I_x/I_y$ or $I_{max}/I_{min}$) which show monotonic declines through time, except in the male femoral midshaft.

**TEMPORAL TRENDS: HUMERAL CROSS-SECTIONAL GEOMETRY:** Unstandardized geometric properties of the humeral 35 percent section are listed in table 7-7, and length-standardized properties are listed in table 7-8. Temporal trends in unstandardized properties generally parallel those in humeral bone length, with both sexes decreasing between precontact preagricultural and precontact agricultural, then increasing (nonsignificantly) between precontact agricultural and contact. The $I_x/I_y$ "shape" ratio shows a monotonic temporal increase in males (significant between precontact agricultural and contact),
but not in females. Theta decreases, then increases, in females; a much weaker (nonsignificant) trend is also characteristic of males.

Length-standardized humeral properties show a pattern of continuous decline in females over all three periods, although none of the differences reach statistical significance. Males also decline between precontact preagricultural and precontact agricultural, in some cases significantly, but then reverse this trend between precontact agricultural and contact periods. Thus, whereas humeri appear to show a pattern of temporal change in mechanical strength similar to femora between the first two periods (decline) and in males between the last two periods (reversal and increase), they show a different pattern in females between the last two periods (continued decrease). Temporal variation in length-standardized polar second moment of area of the humerus is illustrated in figure 7-9.

Results of the two-way ANOVAs (sex, temporal period) for age and all whole bone and cross-sectional geometric properties are given in table 7-9. These essentially reconfirm the patterns of variation noted above. In addition, after length standardization, section properties show the most significant temporal tends in the femoral subtrochanteric section followed by the femoral mid-shaft and the humerus, the latter of which shows no significant temporal effects in this analysis. These results show that even after
SEXUAL DIMORPHISM: The effects of changes in cortical geometry and "size" (length) on sexual dimorphism in the three temporal periods are shown in table 7-10. Only length-standardized cross-sectional properties are included, because of the expected larger overall body size in males. Results are presented as percent differences between males and females with differences \( t \)-tested.

Sexual dimorphism in body size, as assessed by femoral and humeral length, is greatest in the precontact agricultural period and smaller in both contact and precontact preagricultural periods. The very small 2.3 percent dimorphism for bone length in precontact preagricultural femora may be a result of sampling error, although it is close to that calculated for a larger sample from the same region and time period (Larsen, 1982).

Consistent with the results of the two-way ANOVAs reported above, even after length standardization, almost all cross-sectional geometric properties still show significant sexual dimorphism in all temporal periods, with males larger. (The one exception is medullary area, which in any event is a kind of "negative" area property.) Femoral midshaft sexual dimorphism is greatest in the precontact preagricultural and precontact agricultural periods and declines in the contact period. The same is true to a lesser extent in the femoral subtrochanteric section, although some properties (e.g., \( I_{\text{max}} \)) exhibit their greatest decline in sexual dimorphism between precontact preagricultural and precontact agricultural periods. In contrast, sexual dimor-
phism in humeral properties first declines from precontact preagricultural to precontact agricultural, then increases to its largest values in the contact period. This latter finding reflects the continued temporal decrease in humeral properties among females and reversal of this trend in contact males.

Sex differences in cross-sectional “shape” ratios also show some interesting temporal variation. Sexual dimorphism in $I_x/I_y$ of the femoral midshaft first decreases, then increases greatly to almost 19 percent (near significant difference), with males always greater. The ratio $I_{max}/I_{min}$ of the femoral subtrochanteric section is always greater in females but reaches its peak (significant) difference in the precontact agricultural period. The ratio $I_x/I_y$ of the humeral section is 13 percent (significantly) greater among precontact preagricultural females, but this sex difference then declines to essentially zero over the next two temporal periods.

**DISCUSSION**

The first conclusion to be drawn from these results is that the decline in both body size and bone strength relative to body size noted previously between preagricultural and agricultural precontact periods on the Georgia coast (Larsen, 1982; Ruff et al., 1984) does not continue uniformly into the contact period. Based on femoral length, overall body size increases from the precontact agricultural period to near precontact preagricultural levels in both contact period males and females. In general, differences in body size between temporal periods are relatively greater among females than among males. In particular, females show a very large decrease in size in the precontact agricultural period, which also leads to the largest sexual dimorphism in size. These size trends are also generally reflected in the humerus, although not to the same extent as in the femur. If changes in body size largely reflect changes in nutritional status (Larsen, 1982; Ruff et al., 1984), then these results would seem to indicate a general decline, then improvement, in nutritional status through time in the samples studied, particularly females. This “improvement,” however, may have been mainly in nutritional quantity, not quality, as discussed further below.

Relative strength of the femur, standardized for differences in bone length, also first

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**TABLE 7-6**

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<td>95.0</td>
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<td>149.7</td>
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<td>28.7</td>
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* Properties as in table 7-3 and table 7-5.

Significance levels for t-tests between groups and 1-Way ANOVA between groups within sex:

$b p < 0.10$;
$c p < 0.05$;
$d p < 0.01$. 

---

...
declines, then increases through time in both sexes. This pattern is also characteristic of the humerus among males. However, among females, relative humeral strength first declines between precontact preagricultural and precontact agricultural periods and then continues to decline in the contact period. Thus, among females a different pattern of change appears to be characteristic of the upper and lower limbs between the precontact agricultural and contact periods, with the upper limb becoming relatively weaker in the contact period.

It was hypothesized previously (Ruff et al., 1984) that the decline in relative strength of the femur from the precontact preagricultural to precontact agricultural periods was due to a decline in mechanical loadings of the lower limb in the precontact agricultural period brought about at least partly by a decline in general activity levels. “Shape” characteristics of the femur (i.e., second moment of area ratios) were hypothesized to be more reflective of types of activities carried out, and, for example, were shown to be more similar in precontact agricultural samples from the Georgia coast and Pecos Pueblo, New Mexico (Ruff and Hayes, 1983a), than either was to the precontact preagricultural sample from the Georgia coast. The addition of the contact period sample from the Georgia coast, the upper limb as well as the lower limb, and a more extensive comparative base (Ruff, 1987) allows these hypotheses to be further refined and expanded here.

**LOWER LIMB:** Cross-sectional shape differences in the lower limb bones are considered here first because they avoid the problems associated with “size” standardizing of data and because they have been the subject of a
previous comparative study (Ruff, 1987). One finding of the previous study was that males tend to exhibit relatively greater anteroposterior bending strength of the lower limb bones from the midfemur to the midtibia (higher $I_x/I_y$ ratios). However, there is also a systematic variation in this sexual dimorphism related to subsistence strategy, with bone shape sex differences most pronounced in hunter-gatherers, reduced in agriculturalists, and almost nonexistent in industrial populations. Both biomechanical and ethnographic evidence indicate that this association is a consequence of more long-distance travel over uneven terrain in male hunter-gatherers (producing high A-P bending loads near the knee), with a progressive reduction of this sex difference in behavior in agricultural and industrial populations (see discussion in Ruff, 1987). Thus, changes in the $I_x/I_y$ shape ratio of the midfemur through midtibia can be used as an index of relative changes in long-distance mobility.

In the Georgia coast samples studied here, females decline through time in the femoral midshaft $I_x/I_y$ ratio, while males first decline in the precontact agricultural period, then increase in the contact period (table 7-3). Sexual dimorphism in this index declines from precontact preagricultural to precontact agricultural periods, then increases greatly in the contact period (table 7-10). These values for sexual dimorphism are plotted in figure 7-10 along with the ranges and median values for a number of other population samples grouped by subsistence strategy (from Ruff, 1987). As shown here, the Georgia coast precontact preagricultural and precontact agri-

Fig. 7-8. Temporal changes in polar second moment of area ($J$) of the midshaft section of the femur, standardized over $(\text{bone length})^4$ (and multiplied by $10^8$).
<table>
<thead>
<tr>
<th>Property</th>
<th>Preag.</th>
<th>Agric.</th>
<th>Contact</th>
<th>Group differences</th>
<th>1-Way ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
<td>SE</td>
<td>Ag-Pre</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CA</td>
<td>215.7</td>
<td>9.5</td>
<td>196.2</td>
<td>5.8</td>
<td>199.8</td>
</tr>
<tr>
<td>MA</td>
<td>84.4</td>
<td>10.3</td>
<td>69.6</td>
<td>7.7</td>
<td>85.3</td>
</tr>
<tr>
<td>TA</td>
<td>300.0</td>
<td>10.5</td>
<td>265.8</td>
<td>6.2</td>
<td>285.2</td>
</tr>
<tr>
<td>I(_{max})</td>
<td>7450</td>
<td>467</td>
<td>5984</td>
<td>249</td>
<td>6747</td>
</tr>
<tr>
<td>I(_{min})</td>
<td>6128</td>
<td>387</td>
<td>4620</td>
<td>189</td>
<td>5414</td>
</tr>
<tr>
<td>I(_1)</td>
<td>6701</td>
<td>428</td>
<td>5306</td>
<td>200</td>
<td>6272</td>
</tr>
<tr>
<td>J</td>
<td>6874</td>
<td>439</td>
<td>5290</td>
<td>222</td>
<td>5887</td>
</tr>
<tr>
<td></td>
<td>13,597</td>
<td>844</td>
<td>10,603</td>
<td>427</td>
<td>12,161</td>
</tr>
<tr>
<td>PCCA</td>
<td>72.4</td>
<td>2.8</td>
<td>74.2</td>
<td>2.5</td>
<td>70.1</td>
</tr>
<tr>
<td>I(<em>{max}/I(</em>{min})</td>
<td>1.22</td>
<td>0.03</td>
<td>1.31</td>
<td>0.05</td>
<td>1.27</td>
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<td>0.03</td>
<td>1.01</td>
<td>0.03</td>
<td>1.10</td>
</tr>
<tr>
<td>Theta</td>
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<td>10.0</td>
<td>38.5</td>
<td>6.8</td>
<td>54.6</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CA</td>
<td>164.4</td>
<td>7.1</td>
<td>144.7</td>
<td>4.8</td>
<td>151.2</td>
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<td>68.6</td>
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<td>60.8</td>
<td>6.7</td>
<td>59.6</td>
</tr>
<tr>
<td>TA</td>
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<td>8.9</td>
<td>205.4</td>
<td>4.9</td>
<td>210.8</td>
</tr>
<tr>
<td>I(_{max})</td>
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<td>346</td>
<td>3571</td>
<td>161</td>
<td>3727</td>
</tr>
<tr>
<td>I(_{min})</td>
<td>3453</td>
<td>289</td>
<td>2670</td>
<td>12</td>
<td>2813</td>
</tr>
<tr>
<td>I(_1)</td>
<td>4256</td>
<td>356</td>
<td>3202</td>
<td>145</td>
<td>3438</td>
</tr>
<tr>
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<td>3774</td>
<td>277</td>
<td>3035</td>
<td>130</td>
<td>3090</td>
</tr>
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<td></td>
<td>8024</td>
<td>621</td>
<td>6240</td>
<td>260</td>
<td>6540</td>
</tr>
<tr>
<td>PCCA</td>
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<td>3.1</td>
<td>70.9</td>
<td>2.8</td>
<td>71.9</td>
</tr>
<tr>
<td>I(<em>{max}/I(</em>{min})</td>
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<td>0.05</td>
<td>1.35</td>
<td>0.05</td>
<td>1.34</td>
</tr>
<tr>
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<td>1.06</td>
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<td>1.11</td>
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<td>5.5</td>
<td>48.9</td>
<td>3.2</td>
<td>61.8</td>
</tr>
</tbody>
</table>

\(^a\) Properties as in table 7.3.

Significance levels for \(t\)-tests between groups and 1-Way ANOVA between groups within sex:

\(^b\) \(p < 0.10\);

\(^c\) \(p < 0.05\);

\(^d\) \(p < 0.01\).


TABLE 7-8
Temporal Differences in Humeral Cross-sectional Dimensions—Standardized

<table>
<thead>
<tr>
<th>Property</th>
<th>Preag. Mean</th>
<th>SE</th>
<th>Agric. Mean</th>
<th>SE</th>
<th>Contact Mean</th>
<th>SE</th>
<th>Group differences</th>
<th>1-Way ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA/ln²</td>
<td>215.0</td>
<td>11.2</td>
<td>201.2</td>
<td>6.9</td>
<td>204.7</td>
<td>8.6</td>
<td>-13.8</td>
<td>3.5 -10.3</td>
</tr>
<tr>
<td>MA/ln²</td>
<td>83.2</td>
<td>9.5</td>
<td>70.9</td>
<td>7.8</td>
<td>88.3</td>
<td>8.4</td>
<td>-12.3</td>
<td>17.4 5.1</td>
</tr>
<tr>
<td>TA/ln²</td>
<td>298.2</td>
<td>11.8</td>
<td>272.1</td>
<td>6.7</td>
<td>293.1</td>
<td>10.5</td>
<td>-26.1*</td>
<td>21.0 5.1</td>
</tr>
<tr>
<td>I_max/ln⁴</td>
<td>73.8</td>
<td>5.3</td>
<td>62.8</td>
<td>2.9</td>
<td>71.1</td>
<td>4.6</td>
<td>-11.0*</td>
<td>8.3 -2.7</td>
</tr>
<tr>
<td>I_min/ln⁴</td>
<td>61.1</td>
<td>4.8</td>
<td>48.8</td>
<td>2.7</td>
<td>57.3</td>
<td>5.0</td>
<td>-12.3*</td>
<td>8.5 -3.8</td>
</tr>
<tr>
<td>I₁/ln⁴</td>
<td>66.4</td>
<td>4.8</td>
<td>56.0</td>
<td>2.9</td>
<td>66.4</td>
<td>4.3</td>
<td>-10.4*</td>
<td>10.4 0</td>
</tr>
<tr>
<td>I₂/ln⁴</td>
<td>68.6</td>
<td>5.5</td>
<td>55.5</td>
<td>2.4</td>
<td>62.0</td>
<td>5.5</td>
<td>-13.1*</td>
<td>6.5 -6.6</td>
</tr>
<tr>
<td>J/ln⁴</td>
<td>135.0</td>
<td>10.1</td>
<td>111.6</td>
<td>5.1</td>
<td>128.4</td>
<td>9.5</td>
<td>-23.4*</td>
<td>16.8 -6.6</td>
</tr>
</tbody>
</table>

Females

<table>
<thead>
<tr>
<th>Property</th>
<th>Preag. Mean</th>
<th>SE</th>
<th>Agric. Mean</th>
<th>SE</th>
<th>Contact Mean</th>
<th>SE</th>
<th>Group differences</th>
<th>1-Way ANOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA/ln²</td>
<td>179.4</td>
<td>10.8</td>
<td>173.2</td>
<td>7.7</td>
<td>166.6</td>
<td>6.3</td>
<td>-6.1</td>
<td>-6.6 -12.8</td>
</tr>
<tr>
<td>MA/ln²</td>
<td>72.5</td>
<td>8.9</td>
<td>71.7</td>
<td>7.4</td>
<td>65.5</td>
<td>5.6</td>
<td>-0.8</td>
<td>-6.2 -7.0</td>
</tr>
<tr>
<td>TA/ln²</td>
<td>251.9</td>
<td>10.7</td>
<td>244.9</td>
<td>7.0</td>
<td>232.1</td>
<td>7.0</td>
<td>-7.0</td>
<td>-12.8 -19.8</td>
</tr>
<tr>
<td>I_max/ln⁴</td>
<td>53.9</td>
<td>4.3</td>
<td>50.8</td>
<td>2.7</td>
<td>45.3</td>
<td>3.1</td>
<td>-3.1</td>
<td>-5.5 -8.6</td>
</tr>
<tr>
<td>I_min/ln⁴</td>
<td>40.7</td>
<td>3.6</td>
<td>38.4</td>
<td>2.6</td>
<td>34.2</td>
<td>2.5</td>
<td>-2.3</td>
<td>-4.2 -6.5</td>
</tr>
<tr>
<td>I₁/ln⁴</td>
<td>50.4</td>
<td>4.5</td>
<td>45.8</td>
<td>2.7</td>
<td>41.8</td>
<td>3.0</td>
<td>-4.6</td>
<td>-4.0 -8.6</td>
</tr>
<tr>
<td>I₂/ln⁴</td>
<td>44.3</td>
<td>3.4</td>
<td>43.4</td>
<td>2.6</td>
<td>37.5</td>
<td>2.5</td>
<td>-0.9</td>
<td>-5.9 -6.8</td>
</tr>
<tr>
<td>J/ln⁴</td>
<td>94.6</td>
<td>7.8</td>
<td>89.2</td>
<td>5.1</td>
<td>79.5</td>
<td>5.4</td>
<td>-5.4</td>
<td>-9.7 -15.7</td>
</tr>
</tbody>
</table>

a In = length; other properties as in table 7-3 and table 7-5.
Significance levels for t-tests between groups and 1-Way ANOVA between groups within sex:

* p < 0.10;
p < 0.05;
* p < 0.01.

Cultural mean values are close to the median values of their respective subsistence strategy categories, and show the expected decline in sexual dimorphism through time. However, the average contact period sexual dimorphism is much higher, actually above the median value for hunter-gatherers. A closer examination of individual data reveals that the unexpected increase in the mean male value of I₁/ln₁ in the contact period is due mainly to relatively large values among 5 of the 11 male femora (index greater than 1.30), with a distinct break between these and the other six male contact femora (index less than 1.15), also reflected in the relatively large standard error for this property and group (table 7-3). No such bimodal distribution is present in any of the other sex/period groupings.

Thus, these results indicate that among some of the males in the contact period, long-distance travel had increased greatly from the average levels documented prior to contact, while in other males and all females, long-distance travel either stayed about the same or declined. In fact, historic written records for this region indicate that at least some males of the local Guale populations were being pressed into service by the Spanish under the Repartimiento labor system and forced to make periodic long-distance trips to St. Augustine and other localities (Bushnell, 1981; Hann, 1988, personal commun.; Lyon, n.d.; Larsen, this volume). Thus, changes in cross-sectional geometry of the midshaft femur are consistent with certain behavioral changes among these populations known to occur during the mission period.

In the proximal femoral diaphysis (subtrochanteric section), both sexes show a decline through time in the I_max/I_min ratio, an index of "noncircularity" or A-P flattening analogous to the inverse of the traditional meric index (table 7-4). Females always have higher indices, or less circular shafts here than males (table 7-10). This sex difference is also characteristic of other population samples regardless of subsistence strategy, and is most likely a result of increased mediolateral bend-
TEMPORAL CHANGES IN POLAR SECOND MOMENT AREA:
HUMERUS

![Graph showing temporal changes in polar second moment of area (J) of the midshaft section of the humerus, standardized over (bone length')^4 (and multiplied by 10^8).

Fig. 7-9. Temporal changes in polar second moment of area (J) of the midshaft section of the humerus, standardized over (bone length')^4 (and multiplied by 10^8).

...ing loads placed on the proximal femur due to relatively wider hips among females related to childbirth (Ruff, 1987). Here, we hypothesize that the temporal decrease in this index—that is, the increase in circularity of the proximal femoral shaft—observed in both sexes is indicative of a decrease in general activity level. The reasoning behind this interpretation is as follows. Due to its lateral position with respect to the body center of gravity, almost any activity places mediolateral bending loads on the femur which are highest in the proximal diaphysis (Rybicki et al., 1972). However, structural characteristics which reflect adaptation to relatively specialized activities, such as femoral midshaft shape as related to long-distance travel, are not correlated with changes in proximal femoral diaphyseal shape, either across populations (Ruff, 1987) or within the Georgia coast samples themselves. For example, there is no correlation between shape of the femoral midshaft and shape of the subtrochanteric region among contact period males who, as discussed above, appear to show wide variability in long-distance mobility. Thus, because the shape of the proximal femoral diaphysis seems not to reflect specialized mechanical loadings of the lower limb, but should reflect all weight-bearing activity and consequent increase in loads applied to the femur, the most parsimonious explanation is that this shape characteristic is a general index of mechanical loads placed on the hip joint, i.e., an index of general activity level. This interpretation is also consistent with a general worldwide trend toward greater circularity of the femoral subtrochanteric region
in Western industrialized populations relative to preindustrial populations (e.g., Buxton, 1938; Larsen, 1982).

This, then, would indicate that general activity levels were decreasing throughout time on the Georgia coast. However, if this is true, how can we explain the increase in length-standardized cross-sectional areas and second moments of area in these samples in the contact period (tables 7-5 and 7-6)? These results, unlike the cross-sectional shape results, indicate first a decrease from precontact preagricultural to precontact agricultural but then an increase from precontact agricultural to contact in mechanical loads placed on the lower limb as a whole.

One possible explanation is that body weight relative to stature changed systematically for the Guale living under the Spanish mission system. Mechanical loading of the lower limb should be proportional to body weight multiplied by a factor related to activity level. By dividing section properties by powers of bone length to "size standardize" them, we have assumed that body weight/bone length remained constant. However, this may not have been the case. In other words, by length-standardizing these properties, we have actually set up two variables which could have affected cross-sectional properties—activity level and body weight/bone length. Stated mathematically, because section properties $\propto$ body weight/activity level, section properties/bone length $\propto$ (body weight/bone length)-activity level. Because bone length should be highly correlated with stature, this is really equivalent to asking whether body weight/stature (the "ponderal index") of these populations changed in the contact period.

In fact, it is plausible that body weight/stature increased in the missionized Guale relative to previous or nonmissionized contemporary populations due to increased sedentism, a disruption of precontact ways of life, and dietary changes. Larsen (this volume) discusses the aggregation of native populations into centralized villages associated with the missions, and the increasingly focused economy and sedentism characteristic of the contact period (also see Loucks, 1979). Thomas (1988) also noted the relatively "regimented life" of Native Americans associated with missions in Spanish Florida. Stable isotope analysis for these populations (Schoeninger et al., this volume) indicates that the contact period population underwent a definite shift toward increased maize consumption, tying in well with the ethnohistoric descriptions. This dietary change would also be consistent with the greater average stature (bone length) of the contact period sample (table 7-2). The combination of increased se-

### Table 7-9
#### Two-Way Analysis of Variance (Sex, Temporal Period)

<table>
<thead>
<tr>
<th>Property</th>
<th>Femur</th>
<th>Humerus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sex</td>
<td>Period</td>
</tr>
<tr>
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<td>$e$</td>
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</tr>
<tr>
<td>Length'</td>
<td>$e$</td>
<td>$e$</td>
</tr>
<tr>
<td>CD ang.</td>
<td>$-$</td>
<td>$-$</td>
</tr>
<tr>
<td>Ant. ang.</td>
<td>$b$</td>
<td>$e$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Property</th>
<th>Femur</th>
<th>Humerus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sex</td>
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<td>80% section</td>
</tr>
<tr>
<td>CA</td>
<td>$e$</td>
<td>$d$</td>
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<tr>
<td>MA</td>
<td>$b$</td>
<td>$b$</td>
</tr>
<tr>
<td>TA</td>
<td>$e$</td>
<td>$e$</td>
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<td>$e$</td>
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<tr>
<td>$J$</td>
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<tr>
<td>PCCA</td>
<td>$b$</td>
<td>$c$</td>
</tr>
<tr>
<td>$I_{\text{max}}/I_{\text{min}}$</td>
<td>$c$</td>
<td>$c$</td>
</tr>
<tr>
<td>$I_1/I_1$</td>
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<td>$-$</td>
<td>$-$</td>
</tr>
<tr>
<td>CA/ln²</td>
<td>$e$</td>
<td>$e$</td>
</tr>
<tr>
<td>MA/ln²</td>
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<td>$e$</td>
</tr>
<tr>
<td>TA/ln²</td>
<td>$e$</td>
<td>$c$</td>
</tr>
<tr>
<td>$I_{\text{max}}/ln^4$</td>
<td>$e$</td>
<td>$c$</td>
</tr>
<tr>
<td>$I_{\text{min}}/ln^4$</td>
<td>$e$</td>
<td>$e$</td>
</tr>
<tr>
<td>$I_1/ln^4$</td>
<td>$e$</td>
<td>$c$</td>
</tr>
<tr>
<td>$I_1/ln^4$</td>
<td>$e$</td>
<td>$-$</td>
</tr>
<tr>
<td>$J/ln^4$</td>
<td>$e$</td>
<td>$b$</td>
</tr>
</tbody>
</table>

$^a$ Properties as in tables 7-2, 7-3, and 7-5.

Significance levels:

$^b$ $p < 0.10$;

$^c$ $p < 0.05$;

$^d$ $p < 0.01$;

$^e$ $p < 0.001$.

$^f$ No significant sex-period interactions except for femoral thetas.

- Not applicable.
dentism and confinement (with the exception of periodic forced travel for some males) and increased consumption of carbohydrates could have led to relatively greater weight gain in the missionized population. This in turn would increase the body weight/bone length ratio, and thus the length-standardized cross-sectional properties in the lower limb (tables 7-5 and 7-6), despite a generally lower activity level.

This interpretation is consistent with body weight and dietary changes in North American native populations undergoing similar transitions. Hrdlička (1908), for example, found that although obesity is present in all western North American native groups that he observed, it occurs almost exclusively in reservation populations. He pointed out that these populations engage in far less strenuous activities in the shift to a more sedentary lifestyle, thereby resulting in relative gain in body weight. Hrdlička noted:

The men . . . used to be hunters. This mode of life they had to abandon on the reservation, and it is probably the change from their past active outdoor life to the present state of not a little indolence which is the prime cause of their obesity. (1908: 156–157)

In a review of published anthropometric variation of Native American populations, Johnston and Schell (1979) reported that despite a general heterogeneity in these samples there is a tendency for high body weight and high percentage of obesity. Moreover, groups that have moved to an urban setting show a higher frequency of individuals with excessive body weight than their relatives remaining on the reservation (see, for example, Johnston et al., 1978). These data suggest yet more gain in body weight with increase in sedentism.

Although the mechanisms—environmental or otherwise—for weight gain in North American native populations remain unclear, these populations seem to be predisposed to higher body weights, especially as the diets shift to those of nonnative North Americans (Johnston and Schell, 1979), which are high in carbohydrates and fats (cf. McElroy and Townsend, 1979).

Although our interpretation of biomechanical change on the Georgia coast is tentative, it is the only hypothesis which incorporates all of the observed temporal change in cross-sectional geometry of the femur, both cross-sectional shape as well as cross-sectional size.
Fig. 7-10. Sexual dimorphism in two measures of relative A-P to M-L bending strength of the midshaft of the femur, [(male - female)/female] \times 100. Ranges and medians of several population samples arranged by subsistence strategy are shown (from Ruff, 1987, fig. 4) together with the relative positions of the three temporal period samples from the Georgia coast examined in the present study for \( I_x/I_y \) (ratio of second moments of area about x and about y axes). \( D_{ap}/D_{ml} \) (ratio of A-P to M-L external diameters) is also included for comparative purposes (see Ruff, 1987). H-G = hunter-gatherer; AG = agricultural; IND = industrial. Numbers in parentheses indicate number of population samples for each subsistence strategy category.

As stated earlier, geometric properties of femora and humeri in the present study sample tend to follow similar temporal trends, with one major exception. Unlike femora (or male humeri), female humeri continue to decrease in strength relative to bone length in the contact period. Thus, it appears that females in the contact period were placing relatively lower mechanical loads on their upper limbs than in any other period. If the polar second moment of area, \( J \) (a good measure

relative to bone length. As shown below, it is also consistent with upper limb bone data for these samples.

**Upper Limb:** Comparative data for the upper limb bones are unfortunately much more rare than for the lower limb. We are aware of only one previous study which reported on upper limb bone cross-sectional geometric properties in an archaeological sample (Bridges, 1985, 1989). Bridges's study is discussed in the next section of this paper.
of overall strength), is compared between upper and lower limbs, ratios of humeral/femoral strength vary between 0.8 and 0.9 in all periods and sexes, except contact females, where the ratio declines to 0.64 (using length-standardized data, because the samples of humeri and femora are not completely matched [see Materials and Methods]).

The lower strength of contact period female upper limbs relative to their lower limbs is consistent with the hypothesized changes in general activity level and relative body weight among the missionized Guale presented above. Because a relative increase in body weight would affect primarily the weight-supporting lower limb, the decrease in upper limb bone cross-sectional dimensions relative to length could be reflecting a true decrease in activity level, without the counteracting effects of a relatively larger body mass.

The lack of a corresponding decrease in male upper limb bone dimensions relative to length in the contact period could be due to a combination of factors: (1) contact males did not decline in general activity level to the same extent as females, and (2) contact males increased relative use of their upper limbs. Both factors are supported by other skeletal features. First, contact females show by far the most drastic decline in \( I_{max}/I_{min} \), or increase in circularity of the femoral subtrochanteric section of any inter-temporal period comparison (table 7-4), indicating a possible larger decline in activity level. Second, temporal comparisons of humeral cross-sectional shape indicate possible different customary uses of the upper limb among males in the contact period than in earlier periods.

Specifically, relative anteroposterior bending strength (\( I_{z}/I_{y} \)) of the humerus increases in contact males over earlier periods (nearsignificantly from precontact agricultural values and significantly from precontact preagricultural values) (table 7-7). Females always show relatively greater A-P bending strength of the humerus than males (table 7-10), but sexual dimorphism in this characteristic shows a continuous decrease from the precontact preagricultural period to the contact period. There is ethnographic evidence that as agriculture is introduced and then increases in intensity, sex differences in subsistence-related tasks progressively decrease (see Ruff, 1987). Anteroposterior bending loads in the distal humerus would be largely generated by flexion and extension of the elbow. Many subsistence-related tasks, such as field preparation, plowing, and carrying supplies, involve this type of movement. Ethnohistoric records indicate that these tasks were traditionally largely carried out by females in Southeastern native society (Swanton, 1946; Hudson, 1976). However, at least one ethnohistoric account of missionized populations documents pounding of maize into flour as the responsibility of young males (Hann, 1986b; Larsen, this volume).

It is quite possible, then, that males became, either by default or by force, more involved in agricultural tasks during the contact period, particularly among the missionized Indians, partly because earlier male pursuits such as hunting and warfare (Hann, 1986b) were no longer as tenable, and because of the increasingly focused food-producing economy (Larsen, this volume). This would have placed more similar types of mechanical loads on male and female upper limbs, leading to a decline in sexual dimorphism in humeral cross-sectional shape, as well as a possible increase in relative loads placed on the upper limbs in males.

Thus, taken as a whole, the structural data for the femur and humerus presented here support the following hypothesized scenario for the populations of the Georgia coast. First, from the precontact preagricultural to agricultural periods, nutritional level and general activity level declined among both sexes. Long-distance travel declined in males, who also began to take on some agriculturally related tasks. Second, from the precontact agricultural to contact periods, general activity level continued to decline, but due to nutritional changes, particularly higher intakes of carbohydrates (maize), stature and body weight relative to stature increased. Some males engaged in periodic long-distance travel, while other males and females became more sedentary. Males as a whole became more involved in agriculturally related activities.

Other Studies: Bridges (1985, 1989) has reported the data most relevant to the current study. Bridges investigated changes in exter-
nal dimensions and cross-sectional geometry in Archaic and Mississippian period limb bones from the Tennessee River Valley in northern Alabama. Her comparisons are thus most germane to the preagricultural-agricultural comparisons of the present study. Traditional osteometric measurements of external dimensions were carried out on all upper and lower limb long bones in 266 individuals, and cross-sectional properties at five locations in the femoral and humeral diaphyses were determined (through computed tomography) in a smaller subset (n's of 6 to 18 for sex/period groupings).

In general, Bridges’s findings for the Tennessee River Valley are contradictory to those reported here for the Georgia coast with respect to changes in overall bone size (length) and cross-sectional dimensions relative to length, but are more consistent with respect to changes in bone cross-sectional shape. In the Tennessee River Valley sample, all long bones tend to increase in length from Archaic to Mississippian, and some measures of relative strength of the limb bones increase as well. Thus, these populations were apparently becoming larger and, at least in some parts of the appendicular skeleton, relatively stronger with the transition to agriculture. The increases in relative strength are most marked among females near the elbow, and in males in the lower limb as a whole. Males show no changes in upper limb relative strength and female changes in the lower limb are smaller and more inconsistent. The female upper limb changes were interpreted as adaptations to increased mechanical loads resulting from maize grinding in the agricultural period. The male lower limb changes were largely unexplained, although it was hypothesized that they might result from adoption of ball playing games (Bridges, 1985: 138) or simply from a lack of new agricultural tasks placing higher loads on the upper limb as in females. (Changes in bilateral asymmetry of the limb bones noted by Bridges are discussed in Frexia et al., this volume.)

In contrast, changes through time in bone cross-sectional shape, particularly midshaft femoral shape, are similar in the Tennessee River Valley and Georgia coast samples. Relative anteroposterior bending strength of the midshaft femur declines with the transition to agriculture among males of both geographic regions, indicating a reduction in long-distance travel. Sexual dimorphism in shape declines, a finding that is consistent with general hunter-gatherer to agricultural trends (Ruff, 1987). The proximal femoral diaphysis becomes more circular in Bridges’s cross-sectional analysis of females, which is similar to overall temporal trends in the present sample. However, her osteometric analysis of external dimensions in her larger sample does not support this finding, so this result must be considered tentative. (Also, her most proximal section is about 64% of bone length from the distal end, which is not truly a “subtrochanteric” section.) Sexual dimorphism in A-P/M-L bending strength of her most distal humeral location (closest to our 35% section) declines marginally, similar to what we found, but her shape differences between the sexes here are quite small in general, so this similarity must also be considered tentative. (Similar to our findings, sexual dimorphism in relative humeral strength at this location declines markedly through time in the Alabama sample.) In any event, Bridges’s results for proximal femoral and middistal humeral shape are not contradictory to ours.

Thus, although certain effects of the transition from a preagricultural to agricultural subsistence strategy appear to have been different in the Tennessee River Valley and Georgia coast (general body size, relative skeletal robusticity, at least at certain skeletal locations), other effects were more similar (decline in long-distance mobility in males and possibly sexual dimorphism in certain uses of the upper limbs). Some of the specific differences between the studies may be due to methodology. For example, in order to standardize her cross-sectional second moments of area, Bridges divided by the product of maximum fiber length and bone length squared, rather than bone length to the fourth power as was done here. (Our method will tend to reduce changes in cross-sectional dimensions which parallel bone length, while hers will increase them.) We also used two-tailed t-tests for all of our statistical comparisons, and Bridges generally used one-tailed t-tests, which will tend to increase the number of significant differences found. However, there are still some obvious differ-
ences between temporal changes in behavior and possibly diet occurring in the two geographic areas. It may be that preagricultural groups on the Georgia coast lived in a relatively rich (marine and estuarine) environment (see Larsen, 1982, this volume; Reitz, 1988) compared to inland Archaic populations, and that the transition to agriculture involved more of a decrease in nutritional quality, accounting for the difference in general size trends in the two areas. It should be noted that many (although not all) studies of other geographic areas also show a reduction in general body size with the transition to agriculture (see Ruff et al., 1984 and Cohen and Armelagos, 1984, for references). There may have been a heavier dependence on maize during the inland Mississippian period relative to Georgia coast agricultural populations, leading to more discernible effects on female upper limb bones due to maize grinding. This heavier dependence on maize may not have developed until the contact period on the Georgia coast, at which time traditional methods of food production and processing may have changed sufficiently (including more male participation) so that this specific effect is not seen. Regardless, those results of the two studies that are contradictory serve as a warning against overly simplistic reconstructions of "global" changes occurring with environmental transitions which are based on an analysis of only a single geographic area.

Another relevant study of bone cross-sectional geometry is that of Brock and Ruff (1988; also see Brock, 1985), who investigated changes occurring in the femur from A.D. 500 to 1540 in the American Southwest. Results of this study are consistent with those of the present study in that relative A-P bending strength of the femur declines through time in both sexes, indicating less long-distance travel. Overall size (bone length) decreased among females in the last, intensive agricultural stage of the sequence, paralleling the Georgia coast, where females showed the most size reduction with the transition to agriculture. Relative strength increased from the earliest temporal period to a transitional period of cultural and physical disruption, then decreased again in the final intensive agricultural period. As in the present study, the subtrochanteric region became more circular through time among females. However, males first increased in subtrochanteric circularity, then decreased in the last period. Thus, in several respects, temporal/subsistence strategy changes in the Southwest produced effects similar to those seen on the Georgia coast, but the pattern of change in the skeleton was not identical, probably reflecting specific regional variations in environment and behavioral adaptation.

CONCLUSIONS

The size and shape of long bone diaphyses, if viewed from a mechanical perspective, can yield important information on the kinds of forces placed on a bone during life. Overall size of a long bone will depend on both dietary and mechanical factors, but the relative size and shape of a bone are more likely to be related to mechanical factors. Mechanical loads on the weight-supporting lower limb bones will represent a function of both body mass and behavioral use of the limb; mechanical loads on the upper limb will represent a function primarily of behavioral use. Comparative data for the lower limb are more plentiful than for the upper limb; consequently, certain variations in cross-sectional geometry (such as shape of the femoral midshaft) can be interpreted in a behavioral sense with more certainty.

Both upper and lower limb bone data indicate a reduction in both size and relative strength from the precontact preagricultural to the precontact agricultural periods on the Georgia coast. In addition, evidence from the lower limb indicates that both males and females, but especially males, were becoming less mobile, especially with regard to long-distance travel. These changes are consistent with a reduction in dietary quality and an increase in sedentism with the transition to a food economy incorporating agriculture in this region. There is also some evidence for a reduction in sexual dimorphism in use of the upper limb, possibly related to males taking on a few of the tasks associated with food production.

Overall body size in the contact period increased from the precontact agricultural period, possibly reflecting an increase in dietary
quantity, if not quality. Females and some males continued to decline in mobility, but some males, possibly those participating in the Spanish Repartimiento forced labor system, underwent an increase in periodic long-distance travel. Relative body mass to stature may have increased due to a disruption of normal behavioral patterns and a diet increasingly focused on carbohydrates (maize). Male and female differences in use of the upper limb continued to decline, possibly reflecting more male participation in agricultural responsibilities.

These interpretations should be treated as hypotheses which await further testing using both additional skeletal samples and other techniques of skeletal analysis (e.g., see the other contributions to this volume). In particular, analysis of features such as joint articulations (relative size, development of osteoarthritis) and muscle attachment areas, and complementary osteometric data on a larger sample of contact period individuals will help to refine these hypotheses and establish the generality of the trends observed here between the precontact and the contact periods. Using such functional approaches will eventually make possible a more detailed reconstruction of past lifeways, and provide a fuller understanding of the biological and behavioral adaptations of past populations.

ACKNOWLEDGMENTS

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CHAPTER 8. TEMPORAL DECLINE IN BILATERAL ASYMMETRY OF THE UPPER LIMB ON THE GEORGIA COAST

ANNE E. FRESIA, CHRISTOPHER B. RUFF, AND CLARK SPENCER LARSEN

ABSTRACT

Precontact preagricultural, precontact agricultural, and contact period groups from the Georgia coast were evaluated for differential mechanical use of the left and right arms. Bilateral pairs of humeri were radiographed in anteposterior and mediolateral planes, and subperiosteal and cortical breadths were measured at 35 percent of bone length from the distal end. From these linear measurements, bone areas and second moments of area (measures of axial, bending, and torsional strength) were calculated for each side assuming an oval cross-sectional shape.

Bilateral asymmetry in strength of the humerus (right > left) generally decreases through time in these samples. Somewhat different patterns of temporal change are found in males and females. Asymmetry is greatest in precontact preagricultural females and declines most from this period to the precontact agricultural period. Males show more of an even decline in asymmetry from the precontact preagricultural through the contact periods. Sexual dimorphism in bilateral asymmetry is least in the contact period. These results suggest that (1) during the precontact periods females and males were engaged in more dissimilar activities which placed different degrees and types of mechanical demand on the left and right upper limbs, and that activity patterns became more similar in the contact period; and (2) in terms of differential use of the right and left upper limbs, the shift from a hunting and gathering subsistence regime to one that incorporated maize had more of an effect on females, while the arrival of Europeans and establishment of mission centers had more of an effect on males.

INTRODUCTION

Bilateral asymmetry of metric and nonmetric traits is often noted in descriptions of skeletal samples, both human and nonhuman (Hrdlička, 1932; Schultz, 1937; Jolicoeur, 1963; Latimer and Lowrance, 1965; Laubach, 1967; Annett, 1972; Dalen and Olsson, 1974; Garn et al., 1976; Coren and Porac, 1977; Brézard and Bresson, 1983; Ruff and Hayes, 1983b; Koff et al., 1983; Plato et al., 1984; Schell et al., 1985). This pattern is of interest to anthropologists because some degree of asymmetry has been found in every human population studied and has been used as a marker for genetic as well as functional differences between and within populations (Trinkaus, 1978).

Through the study of bilateral asymmetry, certain anatomical patterns can be determined. For example, in limb bone length and weight, human right upper limb bones are consistently larger than left upper limb bones, while the lower limb bones exhibit a pattern of slight left dominance (Latimer and Lowrance, 1965; Ruff and Jones, 1981).

The skeleton is known to respond to mechanical stresses through remodeling of cortical bone areas and through increases in bone density and mass (Nilsson and Westlin, 1971; Watson, 1973; Woo et al., 1981). For this reason, a number of researchers have examined long bone bilateral asymmetries in view of their relationship to differences in mechanical adaptations. More specifically, bilateral asymmetry indicates differential use of the limbs in response to activities which rely on greater use of one limb over the other. Although most investigations have concentrated on experimental data in nonhuman subjects and on measures in athletes (e.g., Buskirk et al., 1956; King et al., 1969; Chinn et al., 1974; Jones et al., 1977), asymmetries in bone mechanical strength in “normal” human samples have also been demonstrated (e.g., Ruff and Jones, 1981; Ruff and Hayes, 1983b; Bridges, 1985; Ben-Itzhak et al., 1988).

This study investigates changes in bilateral asymmetry of structural properties of humeri from precontact and contact period Georgia coastal populations. These changes reflect alterations in mechanical loadings, and thus activity patterns, in this region. Because these samples represent populations from a rela-
were selected from various sex and absence of ability included in the precontact agricultural, periods, including precontact preagricultural, precontact agricultural, and contact. 

<table>
<thead>
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<th>Temporal period/site</th>
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<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Johns Mound</td>
<td>2</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Sea Island Mound</td>
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<td>3</td>
</tr>
<tr>
<td>Deptford</td>
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<td>3</td>
</tr>
<tr>
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</tr>
<tr>
<td>Total</td>
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</tr>
<tr>
<td>Precontact agricultural</td>
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</tr>
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<td>11</td>
<td>22</td>
</tr>
<tr>
<td>Total</td>
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<td>11</td>
<td>22</td>
</tr>
<tr>
<td>Contact</td>
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<td>12</td>
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<td>Pine Harbor</td>
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</tr>
<tr>
<td>Grand total</td>
<td>26</td>
<td>25</td>
<td>51</td>
</tr>
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</table>

* A discussion of the precontact sites is presented in Larsen (1982) and Ruff et al. (1984). Provenience for the contact sites is presented in Larsen (this volume), Saunders (1987), and F. Cook (1980).

MATERIALS AND METHODS

Right and left humeri representing 51 adults from various Georgia coastal localities are included in the study (table 8-1). Specimens were selected for study on the basis of availability and completeness of right and left sides, absence of pathology, and availability of age and sex data. The individuals included in the study were divided into three temporal periods, including precontact preagricultural, precontact agricultural, and contact.

All humeri were radiographed in standardized anteroposterior (A-P) and mediolateral (M-L) planes (see Ruff and Larsen, this volume). Measurements of individual cortices and subperiosteal breadths were taken from radiographs to the nearest 0.05 mm using Helios dial calipers at 35 percent of length from the distal end. Length is defined as the length of the humerus taken from the most proximal point on the head to the most distal point on the lateral lip of the trochlea (fig. 8-1). The 35 percent location was chosen for study because it falls in the region of smallest subperiosteal diameter and also minimizes measurement complications that can arise from radiographic shadowing due to the presence of the deltoid tuberosity proximally and the flexor and extensor ridges distally. This region has also been used in two previous studies of the humerus (Bloom and Laws, 1970; Ruff and Jones, 1981). The use of two planes for measurement of bone breadths eliminates many of the errors in derivation of bone areas from linear measurements (see also Van Gerven et al., 1969).

The measurements taken from the radiographs were used to calculate cortical, subperiosteal, and endosteal areas using the following standard formulas extended for use with data from two planes of measurement (Ruff and Jones, 1981):

Total Subperiosteal Area (TA) = \( \pi(T_{mp}/2)(S_{ml}/2) \)

Endosteal Area (MA) = \( \pi(M_{mp}/2)(M_{ml}/2) \)

Cortical Area (CA) = TA - MA

In addition, the cross-sectional properties of second moments of area about both A-P and M-L axes (I\(_{mp}\) and I\(_{ml}\), respectively), and the polar second moment of area (J) were derived. Their derivations were determined assuming an elliptical cross section (cf. Timoshenko and Gere, 1972) from the radiographic breadths measurements with the following formulas:

\[ I_{ml} = \frac{\pi}{64} (T_{ml}T_{ap}^3 - M_{ml}M_{ap}^3) \]

\[ I_{ap} = \frac{\pi}{64} (T_{ap}T_{mp}^3 - M_{ap}M_{mp}^3) \]

\[ J = I_{ml} + I_{ap} \]

For all formulas:

\( T_{ap} \) = total anteroposterior breadth

\( T_{ml} \) = total mediolateral subperiosteal breadth
\( M_{\text{ap}} = \) anteroposterior endosteal breadth
\( M_{\text{ml}} = \) mediolateral endosteal breadth

Cross-sectional areas and second moments of area are indices of strength at the section location measured. Cortical area is an index of strength in axial loadings. Second moments of area represent strength under bending and torsional loads (Ruff and Larsen, this volume). The property \( I_{\text{ml}} \) is a measure of bending strength in the anteroposterior plane, \( I_{\text{ap}} \) is a measure of bending strength in the mediolateral plane, and \( J \) is a measure of torsional strength and average bending strength in both planes. Two cross-sectional "shape" indices were also evaluated by the ratios of the total A-P to M-L subperiosteal breadths (\( T_{\text{ap}}/T_{\text{ml}} \)) and \( I_{\text{ml}} \) to \( I_{\text{ap}} (I_{\text{ml}}/I_{\text{ap}}) \). In both indices, a ratio close to 1.0 indicates a nearly circular cross section. Thus, ratios that show significant deviation from 1.0 indicate cross sections with relatively greater breadth or bending strength in one plane over the other (>1.0 indicates relatively greater anteroposterior bending strength).

Accuracy of the radiographic estimates of geometric properties was determined by comparison with the data obtained for corresponding sections by direct measurement using the program SLICE (Ruff and Larsen, this volume). Cortical area (CA) and the polar second moment of area (J) were chosen for comparison because each is an estimate using all of the linear bone breadth measurements, and thus should indicate any consistent error between the radiographic and the direct measuring techniques.

Scatterplots for cortical area and polar second moment of area are shown in figures 8-2 and 8-3, respectively. Both CA and J derived from the linear radiographic data were found to be highly correlated with the directly measured values given by the SLICE program (for CA, \( r = 0.83 \); for J, \( r = 0.97 \)). Examination of these figures shows that the bivariate distributions are well described by a line with a slope of 1.0. This finding is also confirmed by least squares, major axis, and reduced major axis regression analysis (Sokal and Rohlf, 1969; Ricker, 1973; Thomas, 1976). On average, the radiographically derived properties slightly overestimate true parameters. However, the overestimate is relatively constant. Thus, bilateral differences between bones using radiographic estimates should accurately reflect differences between true parameters.

Asymmetry between the right and left sides was evaluated using \( t \)-tests for paired observations; differences were considered statistically significant at \( p < 0.05 \). Results are expressed as percent differences to avoid problems associated with variation in body size between sexes and among temporal periods. The percent differences between right and left sides were calculated from the for-
Fig. 8-2. Scatterplot for comparing radiographically estimated and directly measured cortical area (CA) (in mm²). The line plotted is a theoretical line with a slope of 1.0, running through the means of estimated and directly measured properties.

mula: 100 × [(right − left)/right]. Therefore, a percent difference that is greater than zero indicates that the right side is larger. Conversely, a percent difference that is less than zero indicates that the left side is larger. Finally, a one-way analysis of variance was used to investigate differences in asymmetry among the three temporal periods within both sexes.

RESULTS

The overall length of the humerus generally increases in asymmetry throughout the temporal span in both males and females (table 8-2). In the precontact preagricultural group, the difference between right and left sides for both sexes is less than 0.5 percent. This level of side difference continues in the precontact agricultural females. However, there is a higher degree of asymmetry in the contact females in which the difference increases to the statistically significant level of 1 percent. The males of both the precontact agricultural and the contact periods exhibit significant asymmetry in humeral length of approximately 1 percent.

The greatest and most consistent degree of bilateral asymmetry is found in cortical and endosteal areas. Both measures of area show marked percent differences between right and left sides for all time periods (table 8-2). Cortical area in both sexes is significantly greater
on the right side in the precontact preagricultural group as well as the two later groups. There is, however, a marked decline in asymmetry from the preagricultural to the agricultural periods with no further decline seen in the contact period. Endosteal area also shows a high degree of asymmetry which, unlike cortical area, is maintained throughout the temporal span and is larger on the left side than on the right side. Total area, like cortical area, is greater on the right side in the preagricultural period. Bilateral asymmetry in total area then declines in the agricultural period with no further change in the contact period females. Males, however, continue to decline in asymmetry. Overall, the degree of asymmetry in total area is not as great as that in either cortical or medullary areas. Thus, although the right side maintains a somewhat greater cortical bone area through narrowing of the medullary cavity, the relative contraction of the subperiosteal perimeter leads to a decrease through time in asymmetry of axial, bending, and torsional strengths (fig. 8-4).

Asymmetry in bending and torsional strengths of the humerus shows a decline through the temporal span similar to that found in the cross-sectional areas (table 8-3). The preagricultural females exhibit significantly stronger right humeri for torsion and bending in both the A-P and M-L planes. This declines sharply in agricultural period females and remains close to 0 in the contact period. Although asymmetry of these properties declines through time in the males, the
### Table 8-2

<table>
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<td></td>
<td>Right</td>
<td>Left</td>
<td>Side diff.</td>
<td>SE</td>
<td>Percent diff.</td>
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<td>0.7</td>
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<td>1.2</td>
<td>1.1</td>
<td>0.9b</td>
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<td>Contact</td>
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<td>3.0</td>
<td>1.3</td>
<td>1.0b</td>
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<tr>
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<td>15.0</td>
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<td>3.7</td>
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<td>151.6</td>
<td>25.9</td>
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<td>-33.1</td>
<td>16.0</td>
<td>-58.7</td>
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<td>-60.2c</td>
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<td>Contact</td>
<td>47.8</td>
<td>75.7</td>
<td>-27.2</td>
<td>6.8</td>
<td>-58.4c</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Percent difference calculated by the formula: 100 × (right − left)/right. A positive value indicates that the right side is larger; a negative indicates left side is larger.

Significance levels:

- P < 0.05;
- P < 0.01.

The pattern is somewhat different from that in females. In the preagricultural males, strength in torsion and in bending in both planes is greater in the right side than in the left side. With the shift to agriculture, there is a decrease in asymmetry in I\text{ap}, but not a decrease in asymmetry in I\text{ml} or J. These latter two properties show a decline in asymmetry in the contact period relative to the precontact agricultural period. Thus, the contact period males show the least asymmetry in humeral strength of any of the three periods.

Side differences in both of the shape indices (table 8-4) indicate that among preagricultural and agricultural females left humeri are generally more adapted than right humeri for resisting A-P bending. This shape asymmetry disappears in the contact period. Shape asymmetry among males is relatively small except in the I\text{ml}/I\text{ap} index which indicates
that in the agricultural period the right humeri are more adapted for A-P bending.

Table 8-5 shows the one-way analysis of variance within sex, between periods. These results indicate that a significant temporal change in bilateral asymmetry is found in the females, but not in the males, for total subperiosteal area and the second moments of area. Differences between males and females in temporal patterns of change in asymmetry in CA and J are shown in figures 8-5 and 8-6, respectively. In both of these properties, females show the greatest decline in asymmetry between the preagricultural and the agricultural periods. Males, on the other hand, show an overall decline in asymmetry that is relatively more constant.

**DISCUSSION**

The general pattern of right-dominant bilateral asymmetry in the humerus that we have documented for the Georgia coast sample is similar to that reported by other researchers for other human samples (e.g., Hrdlička, 1932; Ruff and Jones, 1981; Ruff and Hayes, 1983b; Bridges, 1985; Ben-Itzhak et al., 1988). This pattern is characteristic of most structural properties in both males and females of all three temporal periods investigated here.

However, the degree of dominance of the right side over the left within the Georgia coast series is not constant, but rather shows a decline throughout the temporal span of the sample. This overall decrease in bilateral asymmetry is associated with changes in subsistence activities and is different in males and females.

In the transition from a lifeway based exclusively on hunting and gathering to that based at least in part on maize agriculture, females generally show much greater biomechanical change than males. Although both sexes exhibit some decline in bilateral asymmetry, the females decline from significant asymmetry in all measures of strength to a relatively small percentage difference between the right and left sides. In contrast, the contact period appears to represent a time of relatively greater change for the males than for the females. For males, all properties (except \( I_{op} \)) decline in asymmetry to a greater extent in that transition than between the first two periods. At contact, females exhibit only slight changes in the percent difference between right and left sides.

These data appear to show that the transition to a subsistence regime based partially on agriculture had a more profound effect upon the differential use of the upper limbs among the females. The greater decrease in asymmetry among the females relative to males results in an increased amount of sexual dimorphism in asymmetry in the agricultural period, particularly in length and in the second moments of area (with the exception of \( I_{op} \)). Sexual dimorphism then decreases in the contact period due to the greater decline in bilateral asymmetry among the males (see table 8-6). Thus, in general, asymmetry in use of the upper limbs in males and females was most dissimilar in the precontact agricultural period and most similar in the contact period.

The temporal patterns of change in humeral asymmetry found in the Georgia coast are generally similar to those reported from the Tennessee River Valley by Bridges (1985). In particular, Bridges (1985) has also shown an overall decline in bilateral asymmetry in the transition to agriculture with the greatest changes taking place within females. However, it is important to note that there is a major difference in the findings of the two
TABLE 8-3
Bilateral Asymmetry in Bending and Torsional Strengths in Males and Females

<table>
<thead>
<tr>
<th></th>
<th>Right</th>
<th>Left</th>
<th>Side diff.</th>
<th>SE</th>
<th>Percent diff.*</th>
</tr>
</thead>
<tbody>
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<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( J_{\text{ml}} )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preagricultural</td>
<td>7893</td>
<td>7372</td>
<td>521</td>
<td>350</td>
<td>6.6</td>
</tr>
<tr>
<td>Agricultural</td>
<td>6474</td>
<td>5949</td>
<td>525</td>
<td>250</td>
<td>8.1</td>
</tr>
<tr>
<td>Contact</td>
<td>6814</td>
<td>6757</td>
<td>57</td>
<td>363</td>
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</tr>
<tr>
<td>( J_{\text{ml}} )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preagricultural</td>
<td>7887</td>
<td>7351</td>
<td>535</td>
<td>446</td>
<td>6.8</td>
</tr>
<tr>
<td>Agricultural</td>
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<td>5670</td>
<td>83</td>
<td>135</td>
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</tr>
<tr>
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<td>6314</td>
<td>6425</td>
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<td>322</td>
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</tr>
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<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( J_{\text{ml}} )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Preagricultural</td>
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<td>3907</td>
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<td>286</td>
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<tr>
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<td>3348</td>
<td>-158</td>
<td>156</td>
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</tr>
<tr>
<td>( J_{\text{ml}} )</td>
<td></td>
<td></td>
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<td></td>
</tr>
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<td>Preagricultural</td>
<td>5056</td>
<td>4404</td>
<td>652</td>
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<td>3578</td>
<td>3736</td>
<td>-158</td>
<td>156</td>
<td>-4.4</td>
</tr>
<tr>
<td><strong>J</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Preagricultural</td>
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<td>1057</td>
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</tr>
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</tr>
<tr>
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<td>-55</td>
<td>655</td>
<td>-0.4</td>
</tr>
</tbody>
</table>
| * Percent difference calculated by the formula: 100 \times (\text{right} - \text{left})/\text{right}.  
| * \( p < 0.05 \).  
| \( J_{\text{ml}} \) denotes bending strength in the anteroposterior plane. 
| \( J_{\text{ml}} \) denotes bending strength in the mediolateral plane. 
| \( J \) denotes torsional strength. 

studies. That is, precontact agricultural Georgia coastal females are generally more asymmetric in terms of size and strength of the humeri than males, while in the Tennessee River Valley, males are always more asymmetric than females.

Bridges (1985) suggested that the decline in asymmetry between right and left sides (and the corresponding increase in sexual dimorphism) in females in the transition to agriculture without a concomitant change in males may be due to the greater role that women played in subsistence-related activities. Bridges suggested that maize grinding—an activity that requires approximately equal strength in both arms, especially in flexion and extension of muscles crossing the elbow joint—may have played a large part in determining humeral morphology. Males, though, took little part in either gathering or agricultural activities, maintaining much the same activity patterns (involving the upper limb) as in the preagricultural period. The Georgia coastal asymmetry data quite clearly support this hypothesis.

The change in degree of asymmetry between hunting-gathering and agriculture in Georgia and the Tennessee River Valley is also generally the same for females. These findings suggest that females of similar subsistence strategy in both regions were engaged in similar activities. The changes among the males in these two regions are not as consistent as those shown for females, however.
Males in the Tennessee River Valley were found to have a relatively high degree of asymmetry in both the preagricultural and the agricultural periods, with only a slight decrease in the agricultural period. As discussed above, these males also exhibit a greater degree of asymmetry than that found among the females. Bridges (1985) suggested that the greater difference in use of the right and left upper limb among males, particularly in the preagricultural period, is due to the use of the atlatl in hunting, an activity that places relatively greater mechanical demands on the right arm than on the left arm. It was suggested that the slight decrease in bilateral asymmetry among the agricultural period males resulted from increased use of the bow and arrow in hunting, thereby placing relatively equal stresses on the right and left arms.

The relatively smaller bilateral asymmetry among the Georgia coastal precontact males suggests that these individuals may not have engaged in hunting to the same extent as the inland Tennessee River Valley group, especially hunting involving the use of the atlatl. As discussed by Larsen (this volume), hunting on the Georgia coast was always secondary in importance to fishing and other activities associated with the acquisition of marine resources. Therefore, it stands to reason that males of these populations would have reduced levels of limb bone asymmetry relative to inland populations. In addition, the transition to a lifeway that included agriculture had only a slight effect on the differential use of the right and left upper limbs, suggesting

### TABLE 8-4
Bilateral Asymmetry in T<sub>ap</sub>/T<sub>ml</sub> and I<sub>ap</sub>/I<sub>ml</sub> in Males and Females

<table>
<thead>
<tr>
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<th>Side diff.</th>
<th>SE</th>
<th>Percent diff. a</th>
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<td>T&lt;sub&gt;ap&lt;/sub&gt;/T&lt;sub&gt;ml&lt;/sub&gt;</td>
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<td>0.02</td>
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<td>0.02</td>
<td>0.05</td>
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<sup>a</sup> Percent difference calculated by the formula: 100 × (right − left)/right.

<sup>b</sup> p < 0.05.

### TABLE 8-5
One-Way Analysis of Variance of Bilateral Asymmetry<sup>a</sup> Among Periods Within Sex

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<th>Females</th>
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</tr>
<tr>
<td>Total area</td>
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<td>d</td>
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<tr>
<td>Cortical area</td>
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<td></td>
</tr>
<tr>
<td>Medullary area</td>
<td></td>
<td></td>
</tr>
<tr>
<td>I&lt;sub&gt;ml&lt;/sub&gt;</td>
<td></td>
<td>c</td>
</tr>
<tr>
<td>I&lt;sub&gt;ap&lt;/sub&gt;</td>
<td></td>
<td>d</td>
</tr>
<tr>
<td>J</td>
<td></td>
<td></td>
</tr>
<tr>
<td>External shape</td>
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<td></td>
</tr>
<tr>
<td>Cortical shape</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Percent difference calculated by the formula: 100 × (right − left)/right.

<sup>b</sup> p < 0.10;
<sup>c</sup> p < 0.05;
<sup>d</sup> p < 0.01.
Fig. 8-5. Temporal comparisons of bilateral differences in cortical area (CA) in males and females.

TABLE 8-6
Sexual Dimorphism* in Bilateral Asymmetry

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<th>Precontact agricultural</th>
<th>Contact</th>
</tr>
</thead>
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<tr>
<td>Length</td>
<td>c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total area</td>
<td>d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cortical area</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medullary area</td>
<td>b</td>
<td>c</td>
<td></td>
</tr>
<tr>
<td>Im</td>
<td>d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isp</td>
<td>b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>J</td>
<td>b</td>
<td>c</td>
<td></td>
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<tr>
<td>Tsp/Tml</td>
<td>d</td>
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<td>Im/Isp</td>
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</tbody>
</table>

*Sexual dimorphism determined by two-sample t-tests between males and females of each temporal period. The tests were performed on the percent difference between right and left sides. Percent difference calculated by the formula: 100 × (right − left)/right.

bp < 0.10;
cp < 0.05;
dp < 0.01.

Ruff (1987) has suggested that increased reliance on agriculture as a subsistence base results in a reduction in the division of labor by sex. The decrease in bilateral asymmetry between males and females from the precontact agricultural to the contact period provides further support for this hypothesis.

With regard to shape asymmetry in right and left humeri, while females of the precontact periods exhibit greater anterior-posterior bending strength on the left side, males generally show greater anterior-posterior bending strength on the right side. In the contact period, neither the males nor the females exhibit any marked difference in relative bending strengths in different planes between the right and left sides. Thus, like general strength asymmetry, sexual dimorphism in shape asymmetry is very low in the contact period. This decline in sexual dimorphism may be only a small shift in activities among the males of this period on the Georgia coast.
due to increased male participation in agricultural activities as a result of forced labor by the Spanish beginning with European contact (see discussion in Ruff and Larsen, this volume).

CONCLUSIONS

Bilateral asymmetry in size and shape of the humerus provides important information regarding the functions and differential use of the upper limb in general. Although overall bone length may be related to general mechanical loadings of a specific skeletal element, cross-sectional geometric properties are more useful for defining particular differential stresses that are applied to the upper limb and activities which involve the greater use of one arm over the other.

The pattern reported here of overall larger size and greater strength of the right side relative to the left side is consistent with that reported in other studies. Comparisons of the temporal periods reveal a decline in asymmetry of the upper limb. We suggest that this decline reflects activity patterns involving change in the use of the upper limbs in the shift to a lifeway that involves agriculture.

Changes in patterns of asymmetry in axial, bending, and torsional strengths indicate that females were affected to a relatively greater degree in the shift to agriculture than males. The resulting increase in sexual dimorphism is consistent with the suggestion that, while females became very involved in new agricultural activities, males maintained patterns of activity (involving the upper limb) not dissimilar from those of the preagricultural period. European contact in the 17th century saw a reduction in sexual dimorphism due in large part to a further decline in bilateral asymmetry among males. This decline in sex-

Fig. 8-6. Temporal comparisons of bilateral differences in polar second moment of area (J) in males and females.
ual dimorphism may reflect an increase in the degree to which males as well as females took part in agricultural activities.

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