

**BODY SIZE AND SHAPE IN INSULAR ENVIRONMENTS  
AND APPLICATIONS OF THE  
ISLAND RULE IN BIOLOGICAL ANTHROPOLOGY**

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the Faculty of the Graduate School  
at the University of Missouri-Columbia

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In Partial Fulfillment  
of the Requirements for the Degree  
Doctor of Philosophy

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by  
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The undersigned, appointed by the dean of the College of Arts and Sciences, have examined the dissertation entitled

BODY SIZE AND SHAPE IN INSULAR ENVIRONMENTS  
AND APPLICATIONS OF  
THE ISLAND RULE IN BIOLOGICAL ANTHROPOLOGY

presented by Colleen B. Young,

a candidate for the degree of doctor of philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

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## **DEDICATION**

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## ABSTRACT

The discovery of small-bodied hominin fossils in 2004 on the island of Flores, Indonesia, unearthed a large debate within biological anthropology. This debate has exemplified that there are questions and research areas that biological anthropologists do not understand about island evolution. To improve understanding on the causes and products of evolution within island areas for biological anthropologists, this dissertation addresses three overarching research areas relevant to the biological anthropology community. The first is an analysis of how primate body sizes vary on islands, with interpretations that are anchored in the evolutionary history of body sizes of primates. Primates that initially evolved body sizes to survive within a frugivorous niche, with elongated life spans to improve survival in unpredictable environments, have body sizes distributed among islands in relation to the presence or absence of these pressures. Smaller islands contain more large, bodied primates overall, whereas larger islands contain more small-bodied ones. Second, an analysis of island fox body size and shape indicates that island foxes have reduced body sizes and divergent skeletal traits compared to mainland, closely related counterparts. Distinct body proportions are likely due to selection because allometric scaling of limb lengths to body mass are divergent for the island fox. Further, the island fox is not a scaled down version of the mainland fox, with limbs decreasing in size at a faster rate compared to the mainland. Last, an investigation on the diversity of two human populations in the Baja California peninsula demonstrates that Amerindians who migrated to and survived in these regions were impacted by ecogeographic pressures in different degrees, likely related to access to resources. Heat-

adapted skeletal traits are apparent in both human populations who inhabited this hot desert, but body size is distinct for the two groups. Body size is smaller for individuals with less access to marine resources and increased susceptibility to periods of drought and starvation. Body size is larger for humans with convenient access to oceanic and terrestrial resources. These studies demonstrate that primates, omnivores, and humans are not immune to the effects of insularity as has been suggested. Rather, interpreting body size and shape alterations requires contextualizing the organism with their evolutionary histories and subsequent interactions within the island areas. Body size alterations are the result of shifting selective pressures from competing with other community members to competing with other individuals within a population over finite resources. As such, body shape can also be divergent compared to closely related mainland counterparts due to adaptation to local ecogeographic pressures. Skeletal traits of organisms need to be interpreted in relation to their migratory journeys and adaptation to local ecogeographic pressures within the island. For humans, contextualizing these variables with cultural and behavioral characteristics is imperative to understand a body size response within a sociocultural omnivorous niche.

## **CHAPTER 1:**

### **INTRODUCTION**

“What method then is open to us who wish to conduct a human experiment but who lack the power either to construct the experimental conditions or to find controlled examples of those conditions here and there throughout our own civilisation?”

-(Margaret Mead p. 7, 1928 “Coming of Age in Samoa”)

Biological anthropologists use and adapt methods developed in the physical, earth, and life sciences to extract and piece together data to better understand the how and why of hominin evolution. However, little attention has been given to studying humans and primates evolving in island environments. This is surprising given the amount of hominin fossils found on islands and that unique human phenotypes are apparent among island ecologies. Further, the historical study of island organisms has yielded profound evolutionary insights (Darwin, 1859; Wallace, 1880). By studying biological variation within island ecologies, biological anthropologists may reach novel insights and conclusions about human evolution.

This goal has become all the more important with the discovery of unique fossils from Liang Bua on the island of Flores, Indonesia, dating to 100—60 kya (Sutikna et al., 2016). Initial discovery of these small-bodied hominins sparked a wave of debates that have lasted almost two decades (Brown et al., 2004; Falk et al., 2005; Larsen et al., 2006, 2009; Schoenemann and Allen, 2006; Martin et al., 2006; Argue et al., 2006, 2009, 2017;

Richards, 2006; Tocheri et al., 2007; Hershkovitz et al., 2007; Bromham and Cardillo, 2007; Gordon et al., 2008; van Heteren, 2008; Lyras et al., 2009; Jungers, 2009, 2013; Jungers et al., 2009a, b; Holliday and Franciscus, 2009, 2012; Brown and Maeda, 2009; Lyras et al., 2009; Weston and Lister, 2009; Montgomery et al., 2010; Aiello, 2010; Kaifu et al., 2011, 2015; Kaifu et al., 2011; Holliday, 2012; Brown, 2012; Kubo et al., 2013; Orr et al., 2013; Montgomery, 2013; Henneberg et al., 2014; Dennell et al., 2014; Van den Bergh et al., 2016; Zeitoun et al., 2016; Baab, 2016; Diniz-Filho and Raia, 2017; Veatch et al., 2019, 2021; Young, 2020; Verhaegen, 2021). Much of these debates stem from ambiguity around the biological meaning of the anatomical features of the fossils. Taken together, unique body proportions, small relative brain to body size, and extremely small stature are outside of the normal range of variation for any extinct or extant hominin (Aiello, 2010), raising the suggestion that it may represent a pathological form, and thereby complicating phylogenetic placement (Martin et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Henneberg et al., 2014).

Anthropologists are not aware of a lot of the foundational literature on island evolution, resulting in misinterpretation of primate evolution on islands. The first misunderstanding within anthropology is that resource limitation measured as available biomass per island area is the most important variable determining body size evolution on islands and defines the island rule. Therefore, Late Pleistocene omnivorous hominins who were able to circumvent these terrestrial resource pressures by extracting marine resources will not follow the island rule (Fitzpatrick et al., 2008; Stone and Fitzpatrick, 2017; Stone et al., 2017, 2019). The second assumption is that the island rule describes similar body size alterations for all taxa in response to the same islands. For instance, if

an elephant dwarfs on island X, a primate (or hominin) should also reduce size on island X, and if the latter does not, it does not follow the island rule (Martin et al., 2006; Schillaci et al., 2009). Last, skeletal traits of an island form should mirror those of mainland counterparts and can be used as phylogenetic signals (e.g., Argue et al., 2016). These assumptions do not account for the dynamic processes that occur when an organism disperses to and evolves within an island and theoretical developments in island science (Raia and Meiri, 2006; van der Geer et al., 2011, 2013; Lomolino et al., 2013; van der Geer, 2014; Itescu et al., 2018).

In the following three manuscripts, I aim to provide a better understanding of island effects on body size and variation for biological anthropology. To do this, I first provide a macroevolutionary analysis on how body size contributes to the species abundance of primates on islands, to understand primary drivers of body size evolution for primates on islands. Then, I demonstrate how dwarfism alters the body size and shape of an omnivorous subspecies, island foxes (*Urocyon littoralis santacruzae*), to aid in interpretations of unique body size and proportions of omnivorous hominin species on islands. Finally, I focus on populations of humans who live near the base of a harsh desert peninsula to understand biological and behavioral responses to these ecogeographic pressures and how maritime adaptations may influence body size and shape of hominins. My overall goal is to elucidate the factors influencing body size and shape evolution of organisms on islands to improve interpretations of body size on islands within biological anthropology and clarify the island rule.

## **Island ecology**

An island is here defined as an area that is circumscribed by boundaries that act to separate it from mainland continental areas, and as a result has distinct community and resource dynamics compared to the mainland (Itescu, 2019). Islands, overall, have reduced resources due to decreased area compared to the mainland, as well as reduced community diversity (types and number of species) due to isolation of the island and decreased evolutionary time (Lomolino et al., 2006, 2009). Higher trophic organisms, such as predators, are less abundant on islands compared to lower trophic ones (Heaney, 1984; Holt et al., 1999; Burness et al., 2001; Meiri et al., 2004). This is because predators require the presence of a viable population of prey for survival, which is less likely on islands with fewer species. Further, predators also need larger areas to support metabolic needs. Organisms with general or flexible diets, such as omnivores or herbivores, are more successful in island areas overall because they are more likely to have resources available within a novel island ecosystem. Consequently, islands often have a decreased ratio of predator to prey species, and decreased community members and resources overall compared to the mainland (Lomolino et al., 2006, 2009, 2012).

Islands have a subset of biodiversity and resources with unique population (within a species) and community (between species) dynamics, which are influenced by the ecogeographic constraints of barriers that surround the island and the size of the island area. Boundaries influence the types of organisms that can immigrate to the island, but also will reduce emigration from the island. Consequently, ecogeographic variables such as island distance from the mainland and island area influence the number and types of species present (MacArthur and Wilson, 1967; Lomolino, 1986, 1990, 1994, 2001;

Lomolino and Wesier, 2001). The farther the island is from the mainland and the smaller the area, the fewer the species will be present.

Islands farther away from the mainland tend to have species with greater dispersal capabilities but fewer species overall compared to islands closer to the mainland due to the difficulties of migrating through the boundary (Lawlor, 1986; Lomolino, 1986; Lomolino et al., 2012). Once an organism migrates to an island, it must subsequently survive within the allotted habitat, because emigration from the area is not as feasible compared to the mainland. The smaller the area is, the fewer resources and habitat complexity present, resulting in fewer species being able to survive and increased extinction rates. Larger areas are able to support increased community diversity (number and types of species) and increased diversification of species over long periods of time due to increased habitat complexity (Williams, 1943; Malyshev, 1969; Whitehead and Jones, 1969; Simberloff, 1970, 1972, 1974, 1976a, 1976b; May, 1975; MacArthur and Wilson, 1976; Simberloff and Abele, 1976; Sepkoski, 1976; Lomolino, 1984a,b, 1986, 2000a, 2001; Lawlor, 1986; Heaney, 2000; Báldi, 2008). As a result, extinction rates are decreased in larger areas. Together, island distance and area influence the number and types of species within an island ecology.

### **Island evolution**

Evolution of island forms is also shaped by the ecogeographic variables of island distance and island area. Spatial boundaries are divergent in ecogeographic traits compared to the island and mainland area, and as a result can act as a type of filter that shapes population and community diversity within an island area. Boundaries are

limiting, pose difficulties for an organism to cross, and therefore shape the gene pool of this isolated population by limiting gene flow. Selection often occurs during migratory journeys because of these boundaries and is known as immigrant selection (Lomolino, 1984, 1993). Traits such as increased dispersal behavior and larger body size are often selected for as they improve the probability of an organism surviving a journey to an island (Price and Sol, 2008; Lomolino et al., 2012, 2013). Consequently, the founding individuals may represent biased samples of the ancestral population (i.e., founder effect; Templeton, 1980). This type of genetic drift can occur within island areas due to biased allele frequencies of the founding population; if certain alleles are over-represented in the founding population, they will become fixed in the island population given enough time (Templeton, 1980).

Additionally, islands are not mirrored ecosystems of the environment an organism originally evolved in, and as a result can exert different selective pressures on phenotypes that are confined in this isolated space. As predation and competition with other community members is reduced in island ecologies, many organisms are initially released from these selective pressures (van der Geer et al., 2011, 2013, 2014). For instance, character displacement is the phenomenon that occurs when the presence of a community member in a similar area influences the phenotype of another (Brown and Wilson, 1956). On islands, with fewer community members, organisms are sometimes separated from species that they competed with in the mainland, and as a result, phenotypes can change due to the absence of competitive species (Simberloff et al., 2000; Meiri et al., 2011).

On islands, there are fewer selective pressures relating to competing with other community members or escaping predation, which enables other selective pressures

relating to migration and surviving with finite resources to become magnified. This often results in founder effects and increased (intraspecific) competition within a population producing divergent phenotypes. Some organisms respond to the pressures of increased intraspecific competition via dispersing and adapting to other island resources thereby taking over an open, unfilled niche (Losos et al., 1998; Losos and Ricklefs, 2009; Losos, 2010). This is because on islands, with shallower evolutionary time and fewer species compared to the mainland, there are often areas that do not have organisms adapted to them yet. Other organisms, though, may respond to increased intraspecific competition by rapidly adapting biological and behavioral characteristics to a niche and evolving novel body sizes and shapes.

### *Body size evolution*

Body size is intimately connected with the dietary and reproductive strategies of an organism (Kleiber, 1932; Damuth, 1993; Charnov, 1991; West et al., 1997; Jeschke and Kokko, 2009), and in island areas (with different population and community dynamics compared to the mainland) organisms often evolve a divergent body size (Foster, 1963, 1964, 1965; Van Valen, 1973; Sondaar, 1977; Case, 1978; Heaney, 1978; Lawlor, 1982; Damuth, 1993; Anderson and Handley, 2002; Brown et al., 2004; Lomolino, 2005; Raia and Meiri, 2006; Meiri, 2007, 2008; Pafilis et al., 2009; Palombo, 2009; Lyras et al., 2010; Jaffe et al., 2011; Lomolino et al., 2012; van der Geer et al., 2013a, 2013b, 2018; Masters et al., 2014; Runemark et al., 2015; Benítez-López et al., 2020). Changes in body size are so prevalent on island areas that an ecological rule was developed to describe it (i.e., the island rule; Van Valen, 1973). First noted by Foster

(1963, 1964, 1965) rodents tend to get bigger and artiodactyls, carnivores, and lagomorphs tend to get smaller on islands. Van Valen (1973) later coined this phenomenon the island rule that defined a more general process where small organisms often get larger (gigantism) and large organisms often get smaller (dwarfism) on a cline that is related to the original body size of the organism (Heaney, 1978; Lomolino, 1985).

An early hypothesis on the cause of dwarfism is that body size alters in response to energetics of an island, such that reduced biomass results in decreased energy available per individual and therefore body size reduction for the species able to survive and reproduce under these resource depauperate conditions, rather than going extinct (Hessee et al., 1951; Kurtén, 1972; Wassersug et al., 1979; Lawlor, 1982). This hypothesis is tied to the idea that body size reduction is directly correlated with carrying capacity, which island area is a proxy for. But subsequent research has identified that island area by itself is a poor predictor of body size alterations (Meiri 2007; Schillaci et al., 2009; Lomolino et al., 2012, 2013; van der Geer et al., 2013, 2016; Athanassiou et al., 2019). Area likely plays a stronger role in influencing the number and types of species and how they interact with each other and the available resources (community-resource dynamics), which in turn has a significant effect on body size evolution on islands (Raia and Meiri, 2006; Lomolino et al., 2012, 2013; van der Geer et al., 2013, 2016).

Dwarfism on islands is likely the result of ecological release and subsequent intraspecific competition over finite resources (Sondaar, 1977; Lomolino, 1985; Raia and Meiri, 2006; Palombo, 2007, 2009; van der Geer et al., 2011, 2013; Lomolino et al., 2012). Upon arriving to an island, an organism is released from the constraints that shaped body size in the mainland but is introduced to novel selective pressures within the

island. How an organism alters its body size in response to islands depends on the adaptive role a particular body size played for the ancestral, mainland organism (i.e., the evolutionary niche; Trappes, 2021). Dwarfism is most apparent in large herbivores on smaller islands, for instance, who evolved a larger body size in the mainland to defend against predation, extract adequate nutrients from resources, and compete with other community members (Illius and Gordon, 1992). In a small island ecology with fewer competitors and predators, body size is less constrained by these selective pressures. Subsequent selective pressures relating to surviving and reproducing in this island ecology are placed on the organism, resulting in body size alterations. Body size dwarfism is prevalent in herbivore species in the absence of predators and other species who compete over similar resources (Palombo, 2007; van der Geer et al., 2011, 2013; Lomolino et al., 2012, 2013; Athanassiou et al., 2019). Distance of the island from the mainland and its area affect the number and types of species within the island, which then play a significant role in influencing the evolution of body size for a particular taxon (Raia and Meiri, 2006; Lomolino et al., 2013).

Gigantism is the phenomenon where small species tend to get larger on islands. Foster (1963, 1964) noted this for rodents, but subsequent observations have discovered gigantism also occurring in insectivores such as a hedgehog relative (*Deinogalerix koenigswaldi*; Freudenthal, 1972) and shrews (*Crocidura russula*; Magnanou et al., 2005), and primates (giant lemurs, e.g. *Megaladapis* and *Palaeopropithecus*; Godfrey et al., 1997). Gigantism is likely the result of immigrant selection and subsequent ecological release in an island ecology. Introduction to the selective pressures of migrating over a boundary paired with the absence of the selective pressures shaping small body size in

the mainland (such as predators) in the colonized island area play the most significant roles in determining enlargement of small species (Lomolino et al., 2012, 2013). The largest individuals of a small species survive migration to distant islands and colonize these areas. Lack of predation and competitors on distant islands enable body sizes that were once constrained by the necessity to hide from predators to further enlarge in size, resulting in gigantism.

### *How does body size evolve on islands?*

The island rule does not simply describe a mainland body size responding to resource availability on an island. Rather, the island rule explains body size alterations on islands that are due to shifting selective pressures following release from mainland selective pressures. This altered body size appears on islands extremely rapidly during initial colonization (< 500 years; Hofman et al., 2015; Rozzi and Lomolino, 2017), and then more slowly over a longer period of time to eventually reach dramatic body size alterations (Lister, 1989, 1996; van der Geet er al., 2013). But, whether body size is selected for directly or a byproduct of other biological factors, such as growth, is unclear (Sondaar, 1977; Palkovacs, 2003). Alterations to growth likely relates to how a specific organism allocates finite energy between surviving and reproducing within an island.

Known as life history tradeoffs, organisms have finite amounts of energy that must be allocated between survival and reproduction (Charnov, 1986, 1990, 1991). Depending on the environment, parental investment trade-offs are made among investing energy in current somatic maintenance or reproductive efforts or delaying investment for future reproduction (Stearns and Koella, 1986; Nylin and Gotthard, 1998; Stearns, 2000;

Brown and Sibly, 2006). When an organism engages in a life history tradeoff to reduce energetic investment in current somatic maintenance, growth ceases at a younger age resulting in a smaller body size. Smaller mammalian species have life histories with increased investment in reproductive rates compared to larger-bodied species worldwide (McNab, 2002). These life histories are often favored in resource-rich environments but also in areas with high juvenile mortality (Nylin and Gotthard, 1998; Ernest, 2003). Increased nutrition from the environment sends hormonal cues to invest energy in reproduction, while increased juvenile mortality also send cues to reproduce before succumbing to mortality; both result in favoring earlier reproduction (Schaffer, 1974; Stearns, 2000).

Both increased investment in reproduction and decreased investment in growth have been theorized as responses to island ecologies that produce small body sizes. MacArthur and Wilson (1967) proposed that life histories that result in a greater number of poor-quality offspring should be most successful in island environments with potentially high mortality rates. In this light, over time, organisms who are able to increase investment in reproduction and maintain viable population levels will prevent extinction more so than others and as a result smaller body size is a successful colonization strategy. Palkovaks (2003), on the other hand, suggested that decreased investment in growth rates paired would increase fitness over longer periods of time in resource-poor island areas and body size is actually a byproduct of selection for reduced growth. These life histories may be favored in resource-poor and unpredictable environments due to periods of starvation exacerbated by seasonal food shortages.

Selection is predicted to favor a delay of reproduction for current somatic investment to increase fitness (McNab, 2002).

Empirical data of extinct and extant island diminutive taxa demonstrate that a reduction of growth speed rather than changes to the timing of growth periods are common but not ubiquitous, and these changes are dependent on the ancestral relatives (van der Geer et al., 2006; van der Geer, 2014; Clauss et al., 2014). Slower growth speed is suggested for a dwarfed elephant (*Palaeoloxodon cypriotes*; Dirks et al., 2012), a dwarfed deer (*Candiacervus*; van deer Geer et al., 2016), a buffalo (*Bubalus depressicornis*; Clauss et al., 2014), and a bovid (*Myotragus balearicus*; Jordana et al., 2012). Though, despite elongated life histories, high juvenile mortality rates (both compared to adults and to mainland taxa) are also paradoxically found in a dwarf deer (*Candiacervus*; van deer Geer et al., 2016) and dwarf elephant (*Elephas falconeri*; Raia et al., 2003). Conversely, fast life history with an earlier age-at-reproduction was observed in the extant dwarf cow (*Bos primigenius taurus*) on Amsterdam Island that underwent rapid body size reduction (Rozzi and Lomolino, 2017). How an island organism allocates energy to survive and reproduce and subsequently alter the speed and timing of growth and development are likely highly taxonomic (Clauss et al., 2014) and environment-specific (Stearns and Koella, 1986; Charnov, 1991), requiring both a genetic and phenotypic analysis (Sear, 2021).

The island rule does not rest on whether body size alterations occur via expedited, delayed, or similar growth trajectories compared to the mainland organism, nor does it depend on whether life history alterations or body size directly are selected for. The island rule explicates a release from one selective pressure in the mainland and the

introduction to a novel selective pressure in the island that influences body size of a taxon. The underlying mechanisms and types of selective pressures that influence an organism in an island ecology are context-specific and relate to the original adaptive role the body size played in the mainland context. Interpretations of primates, hominins, and humans on islands that evoke the island rule need to first clarify the types of selective pressures (or evolutionary niche) promoting a particular body size in the mainland counterpart. Subsequent interpretations of body size alterations should then account for the novel selective pressures the island populations are under following release from these mainland selective pressures. Only then can biological anthropologists make more informed interpretations of body size responses on islands within the framework of the island rule and gain deeper insights on body size evolution as a whole.

### *Primate body size evolution on islands*

Organisms respond to island ecologies in diverse ways, because of differential evolved biological and behavioral strategies (Lewontin, 1965), and how the island rule applies to primates is unclear. For instance, despite evidence of subfossil giant lemurs in Madagascar (Godfrey et al., 1997), small-bodied primates do not tend to get larger on islands overall. This is surprising given the numerous islands that small-bodied tarsiers, galagos, and lorises occupy. Small-bodied primates may not get larger on these islands because many of these primates did not migrate to islands at all but are the result of vicariance on land bridge islands after glacial expansions (Harcourt, 1999). Therefore, their body sizes were not subjected to immigrant selection, which is related to gigantism in other organisms on islands (Lomolino et al, 2012). Giant subfossil lemurs in

Madagascar, though, may be the result of immigrant selection during early migration over the Mozambique Channel and subsequent ecological release (Godfrey et al., 1997). This idea is supported by research suggesting that members of the family Cheirogaleidae are actually phyletic dwarfs from larger lemuriform ancestors (Masters et al. 2014). Large-bodied lemuriforms may have colonized and adapted to the resource rich environment of Madagascar, but over time, increases in intraspecific competition in this rich arboreal environment drove secondary reduction in body size in these taxa.

Further, while some research has noted subtle body size reduction in a small sample of primates on islands (Bromham and Cardillo, 2007; Welch, 2009; Montgomery, 2013), large-bodied primates generally do not demonstrate predictable or appreciable body size reduction among small island areas (Schillaci et al., 2009). This may indicate that large body size evolved in primates in mainland areas not as a response to evade predation or outcompete other community members as has been suggested (i.e., Anderson, 1986; Isbell, 2005). Instead, early primates likely evaded terrestrial predators and other community members via adapting to an arboreal frugivorous niche. Body size evolution in primates may relate more to reducing mortality rates by increasing fitness through investing in growth in this niche.

Primates evolved in a dietary niche dependent on nutrient-dense foods such as fruits and seeds, which are highly seasonal and sometimes unpredictable (Gogarten et al., 2012). Jones (2011) suggested that body size evolution in primates may be a byproduct of life history elongation to support multiple births over an extended period to increase fitness in this niche. A life history strategy that increased current somatic investment to reduce adult mortality and therefore spread out the number of offspring over many years

(to hopefully reproduce in a “fruitful” year) likely increased fitness for primates (Blomquist, 2009; Jones, 2011). The elongated life history of primates likely improved survivorship and reproductive success in unpredictable environments (Jones, 2011). Subsequent enlargement of body size in monkeys and apes is therefore related to increased longevity and an elongated life history strategy.

On islands, large primate body size may be less affected by the presence of terrestrial interspecific competitors or predators but by resource availability and predictability and competition with other arboreal frugivorous species (such as other primates). Larger body sizes with elongated life histories and increased investment in survival should be expected in resource-poor unpredictable island ecologies, such as small island areas; small island areas may actually contain the pressures driving body size in mainland primates. Body size reduction in primates should occur in areas with a release from the constraint of unpredictable food and in areas with rich resources and the addition of a novel selective pressure, such as increased competition among these resources, increasing mortality rates. Reproducing at a later age in these instances results in decreased fitness. Therefore, I suggest that mortality patterns are now shifting to favor earlier age-at-reproduction and subsequent smaller body size.

### *Body shape evolution*

When body size changes occur, sometimes novel skeletal traits arise (Foster, 1965; Ambrosetti, 1968; Leinders and Sondaar, 1974; Sondaar, 1977; van der Geer, 2005, 2014; Raia, 2009). These traits can result due to genetic drift, allometry (changes in shape with size), or may represent adaptations to island resources (Marshall and

Corruccini, 1978). Cranial shape changes proportional to changes in size are found in dwarfed elephants, for instance (Sondaar and Boekschoten, 1967; Roth, 1992; Palombo, 2001). These changes follow mainland allometric patterns suggesting that the decreased pneumatization of the skull of the dwarf elephant (*Elephas falconeri*) does not represent an adaptation but just a change in shape related to decreased cranial size (van der Geer et al., 2018). Relatively larger molars (hypodonty) and missing premolars are also often found in dwarfed forms and likely represent changes in skeletal traits due to changes in size (Sondaar, 1977).

Allometric trends for island forms can sometimes be divergent compared to mainland ones, though, solely due to changes in growth (Pélabon et al., 2013). Because changes to size are likely related to changes in growth of the island organism (Gould, 1977; Clauss et al., 2014), differences in allometric scaling of a trait to body size can occur and not necessarily reflect selection for differences in this trait (White and Gould, 1965; Alberch et al., 1979; Ergest et al., 2012). Changes to the growth of body size can influence the development of a trait and result in differential allometric scaling for an island form (Pélabon et al., 2013). Changes in the timing and rate of growth has been proposed as contributing to the differential scaling of brain to body size of *Homo floresiensis* compared to other hominins (Weston and Lister, 2009). The differential allometric scaling of the brain of the small-bodied hominin may be due to changes in the pattern and timing of growth related to body size evolution in the island ecology, which is why the scaling trends do not follow mainland *Homo erectus* patterns.

Changes to skeletal traits may also arise as an adaptive response to novel island selective pressures. Dwarfed hippos, for instance, have anatomical reorganization of the

skull that do not follow mainland allometric scaling trends and likely represent selection for cranial shape changes (van der Geer et al., 2018). Changes in limb length, orientation, and proportions are also extremely common in dwarfed mammals (such as *Candiacervus* and *Hoplitomeryx* (deer), *Hippopotamus* (hippo), *Stegodon* (stegodont), and *Myotragus* (goat; van der Geer, 2005, 2014). Dwarfed artiodactyls tend to have relatively reduced distal limb segments that may reflect adaptation to different locomotive behaviors in novel island terrain (Sondaar, 1977). Reduction of distal limb elements of a Pleistocene dwarfed carnivorous canid (*Cynotherium sardous*) may also reflect an adaptation for catching smaller-bodied prey on the island of Sardinia (Lytras and van der Geer, 2006). Changes in body proportions and scaling of limb lengths to body size often result as adaptations to novel island ecologies (van der Geer, 2014; Young, 2020).

#### *Human body size evolution on islands*

The hominin terrestrial bipedal body form began to emerge at least 3 mya with *Australopithecus* and is associated with a niche shift for hominins (Muhlenbein and Flinn, 2001; Grabowski et al., 2015). As hominins became terrestrially dependent, compared to other apes, a dietary shift from primarily fruit and C<sub>3</sub> resources to seeds, tubers, nuts, and C<sub>4</sub> grasses are associated with a divergent life history strategy and bipedal adaptations (Muhlenbein and Flinn, 2001; Unger and Sponheimer, 2011; Sponheimer et al., 2013). Further, increased competition with other community members and predation in the terrestrial ecology of East Africa also likely exerted selective pressures on hominins.

The characteristic tall stature of modern humans appeared with *Homo erectus* at about 2 mya with an elongation of the lower limbs and is associated with a social omnivorous dietary niche with increased reliance on meat and elevated metabolic rates (Pontzer, 2017). Elongated limbs are more calorically efficient than shorter limbs in mammals and are associated with increased locomotor efficiency and range expansion (Polk, 2004; Pontzer, 2007, 2017). Range expansion was likely beneficial for these social omnivores with expanding brains and sociocultural complexity who required increased availability of nutritious foods for individual and group survival (Domínguez-Rodrigo et al., 2005; Antón et al., 2014; Kuzawa et al., 2014; Hublin et al., 2015; Plummer and Finestone, 2017). Increased ranges may also have been beneficial at avoiding predation (Polk, 2004).

Later, anatomically modern humans emerged within a niche mediated by further sociocultural interdependence within an omnivorous diet at about 200,000 years ago (Fuentes, 2016). During this time, an earlier age-at-weaning and a further elongated juvenile period with low interbirth intervals supported increased cognitive development and social complexity (Muhlenbein and Flinn, 2001). This modern life history likely evolved in response to the cultural and dietary niche humans adapted to that depends on group support and provisioning (Kaplan et al., 2000; Hawkes et al., 2017). An elongated juvenile period paired with an expedited weaning period alleviated nutritional burdens on the mother. But this was only made possible by increased energetic investment by non-maternal family and community members (alloparenting) to support increased survivorship of the offspring following earlier-weaning periods. Human mothers are

uniquely able to sustain high reproductive and somatic investment with this life history strategy and socioculturally-influenced niche.

High levels of developmental and behavioral plasticity within this life history strategy among populations results in incredible variation of human body size (Kuzawa and Bragg, 2014). Environmental and social cues send signals early in development that can alter the speed and time of growth that influences adult body size (Stearns and Koella, 1986; Sears, 2021). Generally, holding all else constant, resource-poor and stressful environments early in life may act to reduce growth and delay reproduction resulting in a smaller body size. Resource-rich and predictable environments may increase growth speed and result in an earlier age-at-reproduction producing a larger body size overall. In addition, mortality rates influenced by these social and environmental cues can also influence life history strategies. For instance, populations with high rates of extrinsic juvenile mortality can exhibit expedited growth with an earlier age-at-reproduction and cessation of growth and smaller body sizes (Walker et al., 2006).

Similar to other species, when humans migrate to and colonize island and island-like areas, body size is likely highly responsive and influenced by novel pressures related to shifting social and environmental dynamics introduced during migration and colonization of an island. Island ecological characteristics such as isolation and area can influence how humans interact with each other and the environment that may result in alterations in growth and body size. Reduced access to predictable and stable resources via reduced species diversity and resource abundance in smaller island areas may act to reduce growth. Increased extrinsic juvenile mortality from social or environmental

pressures may also act to reduce body size via an earlier cessation of growth. Unlike other organisms though, humans use sociocultural adaptations and may circumvent the ecogeographic constraints imposed by isolation and island area. This idea is often used as a talking point among anthropologists as reasons why humans and hominins should not follow the island rule.

Humans construct a niche with sociocultural networks to adapt to diverse environments, and in some instances, adapt to finite resources and isolated ecologies with complex trade and social dynamics that potentially alleviate local resource restrictions (Wiessner et al. 2002; Hill et al. 2011; Laland et al. 2016). The ability of humans to efficiently migrate, communicate, extract, and trade resources with nearby areas may significantly reduce resource depression and mortality rates and/or increase resource availability (e.g., the Kula Ring; Malinowski, 1920). Though, human sociocultural adaptations that alleviated a constraint in one respect may have unintended impacts and introduce humans to other constraints. For instance, colonization of the Polynesian islands of Mangareva by humans in the 13<sup>th</sup> century is associated with a rapid decline in seabird populations followed by an increase in rats and fire-adapted plants (Kirch et al., 2015). Seabird feces are a critical source of nitrogen, especially on oceanic islands with volcanic, nutrient-poor, soils. The extirpation of seabirds caused the unintended consequence of poor terrestrial productivity, which was later rectified by introducing regulated fire regimes to the novel crops. Humans respond in diverse ways to island environments that have varying resource-availability and population dynamics. How these short- and long-term sociocultural adaptations act to influence population dynamics and selective pressures of human phenotypes is not clear.

Stature reduction is apparent for some humans in island and island-like (insular) environments. Convergent body size reduction, where adult stature is less than 155 cm, is found in Andaman, Philippines, Indonesian, and Papua New Guinea islanders, as well as in isolated mainland rainforest groups, including the African Bambenga, Bambuti, and Batwa, and the Hiwi of Venezuela. The affinity, causes, and adaptive advantages of these phenotypes were debated (Cavalli-Sforza, 1986; Diamond, 1991; Migliano, 2005; Perry and Dominy, 2009; Migliano et al., 2013). But, the short stature in these various groups is likely the result of selection for earlier age-at-reproduction or a reduced growth speed in response to population dynamics of these isolated groups (Walker et al., 2009; Migliano et al., 2013; Rozzi et al., 2015).

The fact that small-bodied humans achieve small size in island and island-like environments via early cessation of growth has been used as evidence that humans do not follow the island rule (Berger et al., 2008; Fitzpatrick et al., 2008; Anonymous, pers. comm.). Why selection for altered life history strategies that influences body size in response to island ecologies does not qualify as the island rule is unclear. It is likely related to the erroneous logic that the island rule explains organisms evolving divergent body size solely due to resource limitations, which as explained in depth above, is not the island rule. Under this logic, if small-bodied humans achieve smaller body size because of selection for earlier age-at-reproduction, they are not following the island rule, because it is not due to selection for smaller size directly under resource limitations. As elongated life histories with later age-at-reproduction are a part of the unique human evolutionary niche, alterations that involve a reduction of the juvenile period indicates a change in selective pressures on this life history strategy. This aligns with the definition of the

island rule being alterations to body size in an island area as a response to changing selective from inter- to intraspecific competition. The island rule makes no definitive claims about *how* an organism reaches an alternate body size nor whether selection is occurring directly on body size or life history traits that influence body size.

### *Human body shape evolution on islands*

Body shape, such as limb proportions and hip breadth, in humans generally follows latitudinal clines beginning at a young age indicating that thermoregulation is likely a selective force behind these skeletal traits worldwide (Bergmann, 1847; Allen, 1877; Ruff, 2002; Cowgill et al., 2012). Limb length and proportions, including the brachial (radius / humerus) and crural (tibia / femur) indices, are generally longer and higher in lower latitudinal groups with warmer climates. Further, hip width (bi-iliac breadth) is generally narrower in lower latitudinal, warmer climatic groups. A narrower hip with distally elongated limbs increases surface area to volume ratios and effectively cools the body (Ruff, 1991). Conversely, wider bi-iliac breadth and shorter limbs improves heat retention in cooler climates.

Many individuals on island environments display unique body proportions, outside of what is predicted by these climatic models (Bergmann, 1847; Allen, 1877; Ruff, 1994, 2002). The Jomon in Japan and Pacific Islanders, for instance, have body proportions that do not follow ecogeographic predictions (Houghton, 1996; Leach, unpubl. 2006; Temple & Matsumura, 2011). The Hokkaido Jomon were an isolated hunter-gathering group in northern Japan who had bodies characterized by high intramembral (within limb) indices following trends found in humans in warm tropical

environments (Allen, 1877; Yamaguchi, 1989; Kato & Ogata, 1989). Further, Pacific Island groups have, paradoxically, cold-adapted body types with high body mass and wide bi-illiac breadth (Leach unpubl., 2006; Houghton, 1996). Human groups, therefore, express diverse shape in insular environments that do not always follow expected patterns of adaptation to the immediate ecology.

Humans use cultural and social adaptations to navigate through terrain boundaries with significant biological constraints, such as oceans, mountain tops, and deserts. Therefore, humans are able to migrate to and from most areas on earth. Migration over an extreme environment has the potential to shape patterns of human variation if resources, climate, or terrain, within this boundary act to limit survivability. Work to understand the unique body proportions of the Jomon and Pacific Islanders have evoked the effects of immigration and founder effects on these phenotypes. Temple & Matsumura (2011) suggest that the Jomon warm-adapted limb proportions on a frigid Japanese island may have evolved outside of the local ecology and subsequent founder effects within this island resulted in divergent body shape for the cold climate. Further, the cold-adapted body form of Pacific Islanders, including high body mass, may have been advantageous while crossing the vast Pacific Ocean: bodies able to withstand long periods of starvation and high rainfall survived the journey more so than others (Leach, unpubl. 2006; Houghton, 1996).

These interpretations are supported by a recent analysis by Roseman and Auerbach (2015) on latitudinal patterns of human body shape worldwide. They found that when population structure was included in statistical models that predict body shape from latitude, the predictive power of these models significantly improved. Specifically,

distal limb element lengths and bi-iliac breadth are better predicted by both population structure and latitude. In island areas that were founded by a population of humans who may have had skeletal traits that adapted to ecogeographic conditions outside of the island ecology, population structure may play a significant role in contributing to subsequent adaptation of skeletal traits in the island ecology. Skeletal traits in humans in these island ecologies may diverge from what is predicted by local latitude alone.

Human body shape may be a fruitful avenue for understanding the island rule and its applications to humans in general. If humans are significantly impacted by immigrant selection and founder effects, similar to organisms who undergo gigantism, the island rule may better be explained for humans as alterations in body shape. Humans' ability to navigate across oceanic barriers likely introduces us to novel ecogeographic selective pressures relating to climate, water, and resource limitations. How humans survive these dangerous, unpredictable, and novel journeys and contribute to the population diversity of an island is not entirely understood.

## Dissertation layout

The layout of the dissertation is as follows. Chapter 2 will focus on how body size of primates is patterned among various island areas. I use the species-area relationship of primates on islands to assess how body masses contribute to primate species abundance among islands of different areas. I guide my interpretations using island biogeography to assess how species abundance of primates on islands are influenced by area and related to island ecologies. I show how body masses of primates are distributed and related to island biogeography. I found that small body masses of primates are more prevalent and

concentrated on the biggest islands, whereas large body masses are more abundant and evenly distributed across all islands (small to large). Further, small-bodied (<2700 g) primates do not increase size on small islands, and large-bodied (>2700 g) primates do not decrease size on small islands. This study helps clarify the island rule and provides evidence that population and community dynamics around finite resources play a more prominent role in shaping body size on islands than does absolute biomass of an island.

As noted, islands affect body size and understanding how this process influences skeletal traits can shed light into understanding how hominins adapted to islands. One of the biggest challenges in interpreting small-bodied hominin fossils is understanding the evolutionary meaning underlying specific skeletal traits, which I address in Chapter 3. By using an animal model within a similar dietary niche as Late Pleistocene hominins, I directly compare the omnivorous island foxes to their mainland counterparts. I specifically explored intra (within limb) and interlimb (between limb) indices to infer if there are changes in limb proportions for omnivores as a result of adapting to an island ecology. Results indicate that the island fox has significantly smaller body masses and limbs than the mainland fox. Further, the island fox has different static (across adults) allometric trends than the mainland fox. These allometric alterations produce significantly different humerofemoral, intermembral, and brachial indices for the island fox compared to the mainland fox. These changes are likely due to the island fox adapting to the unique island ecology. The island fox is not just a scaled down version of the mainland fox. Findings from this study can help us better understand the impact islands have on hominins, like *H. floresensis*, who had distinct limb proportions compared to nearby mainland hominins such as *H. erectus*. Island omnivores who

supplement terrestrial diets with marine resources can still exhibit altered body size and shape compared to mainland forms that reflect adaptation to the local isolated ecology.

Humans may be particularly immune to the effects of island ecologies due to our cumulative cultural evolution that aids in survival, mortality reduction, and potentially circumvents local environmental pressures of isolated areas. I explore this idea in Chapter 4 as I compared the behavioral dynamics and biological traits of two populations of marine-hunter-gatherers in the Baja California Peninsula. I use Baja California Peninsula because ethnohistoric, archaeological, and skeletal data indicate long-term isolation for most of the Holocene, and it is an isolated area significantly influenced by freshwater and resource scarcity. To identify how humans behaviorally navigated around finite resources and the corresponding impacts this had on the formation of human variation, I assessed the cross-sectional geometry of limbs and body size and shape of two populations in the peninsula and compared these results to worldwide samples of humans. I found that humans with better access to marine and water resources were less impacted by the effects of finite resources but still evolved a body shape reflecting long-term isolation in a hot climate. Humans with less convenient access to both marine and terrestrial resources had heat-adapted bodies but also bodies that reflected nutritional and aridity stresses. Humans, and hominins, are able to circumvent local energetic constraints but are still impacted by ecogeographic variables such as climate, and in areas with less access to resources, are impacted by resource restrictions.

## Literature Cited

- Aiello LC. 2010. Five years of *Homo floresiensis*. Am J Phys Anthropol 142: 167–179.
- Alberch P, Gould SJ, Oster GF, Wake DB. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 1:296–317.
- Allen JA. 1877. The influence of physical conditions in the genesis of species. Rad Rev 1:108-140.
- Ambrosetti P. 1968. The Pleistocene dwarf elephants of Spinagallo (Siracusa, South-Eastern Sicily). Geol Rom 7:277-398.
- Anderson CM. 1986. Predation and primate evolution. Primates. 27:15–39.
- Anderson RP, Handley CO Jr. 2002. Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. Evolution 56:1045–1058.
- Argue D, Donlon D, Groves C, Wright R. 2006. *Homo floresiensis*: microcephalic, pygmy, *Australopithecus*, or *Homo*? J Hum Evol 51: 360–374.
- Argue D, Groves CP, Lee MSY, Jungers WL. 2017. The affinities of *Homo floresiensis* based on phylogenetic analyses of cranial, dental, and postcranial characters. J Hum Evol 107:107–133.
- Argue D, Morwood MJ, Sutikna T, Jatmiko, Saptomo EW. 2009. *Homo floresiensis*: a cladistic analysis. J Hum Evol 57:623–639.
- Baab K. 2016. The place of *Homo floresiensis* in human evolution. J Anthropol Sci 94:5–18.

Benítez-López A, Santini L, Gallego-Zamorano J, Milá B, Walkden P, Huijbregts MAJ, et al. 2020. The island rule explains consistent patterns of body size evolution across terrestrial vertebrates. *Nat Ecol Evol* 5:768–786.

Berger LR, Churchill SR, De Klerk B, Quinn RL. 2008. Small-bodied humans from Palau, Micronesia. *PloS One* 3:e1780.

Bergmann C. 1847. About the relationships between heat conservation and body size of animals. *Goett Stud* 1:595-708.

Berry RJ. 1964. The evolution of an island population of the house mouse. *Evolution* 1:468-483.

Blomquist GE. 2009. Trade-off between age of first reproduction and survival in a female primate. *Biol Lett* 5:339–342.

Bromham L, Cardillo M. 2007. Primates follow the “island rule”: implications for interpreting *Homo floresiensis*. *Biol Lett*. 3:398–400.

Brown JH, Lomolino MV. 2000. Concluding remarks: historical perspective and the future of island biogeography theory. *Glob Ecol Biogeogr* 9:87–92.

Brown P. 2012. LB1 and LB6 *Homo floresiensis* are not modern human (*Homo sapiens*) cretins. *J Hum Evol* 62: 201–224.

Brown P, Maeda T. 2009. Liang Bua *Homo floresiensis* mandibles and mandibular teeth: a contribution to the comparative morphology of a new hominin species. *J Hum Evol* 57:571–596.

Brown P, Sutikna T, Morwood MJ et al. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 403, 1055–1061.

Case TJ. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*. 59:1–18.

Cavalli-Sforza LL. 1986. African pygmies: An evaluation of the state of research. *African Pygmies*, ed Cavalli- Sforza LL. Academic Press, Orlando, FL, pp 361–426.

Charnov EL. 1990a. On evolution of age of maturity and the adult lifespan. *J Evol Biol* 3:139–144.

Charnov EL. 1990b. Relative size at the onset of maturity (RSOM) is an interesting number in crustacean growth (Decapoda, Pandalidae). *Crustaceana* 59:108–109.

Charnov EL. 1991. Evolution of life history variation among female mammals. *Proc Natl Acad Sci USA* 88:1134–1137.

Damuth J. 1993. Cope’s rule, the island rule and the scaling of mammalian population density. *Nature* 365:748–750.

Darwin CL. 1859. *On the Origins of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. PF Collier & son, New York.

Diamond J. 1991. Anthropology. Why are pygmies small? *Nature* 354:111-112.

Diniz-Filho JAF, Raia P. 2017. Island Rule, quantitative genetics and brain–body size evolution in *Homo floresiensis*. *Proc Royal Soc B*. 284:20171065.

- Ergest CK, Bolstad GH, Rosenqvist G, Endler JA, Pelabon C. 2011. Geographical variation in allometry in the guppy (*Poecilia reticulate*). *J Evol Biol* 24.
- Ergest CK, Hansen TF, Le Rouzic A, Bolstad GH, Rosenqvist G, Pelabon C, 2012. Artificial selection on allometry: change in elevation but not slope. *J Evol Biol* 25.
- Falk D, Hildebolt C, Smith K, Morwood MJ, Sutikna T, Brown P, et al. 2005. The brain of LB1, *Homo floresiensis*. *Science* 308: 242–245.
- Firth R. 1961. Suicide and risk-taking in Tikopia society. *Psychiatry* 24: 1-17.
- Fitzpatrick SM, Nelson GC, Clark G. 2008. Small scattered fragments do not a dwarf make: biological and archaeological data indicate that prehistoric inhabitants of Palau were normal sized. *PLoS One* 3:e3015.
- Foster JB. 1963. The evolution of native land mammals of the Queen Charlotte Islands and the problem of insularity. Ph.D. diss., University of Columbia, Vancouver.
- Foster JB. 1964. The evolution of mammals on islands. *Nature* 202:234-235.
- Foster JB. 1965. The evolution of mammals on the Queen Charlotte Islands, British Columbia. *BC Prov Mus Nat Hist Anthropol Occas Pap* 14:1-130.
- Gordon AD, Nevell L, Wood B. 2008. The *Homo floresiensis* cranium (LB1): size, scaling, and early Homo affinities. *Proc Natl Acad Sci USA*. 105:4650–4655.
- Hanna E, Cardillo M. 2014. Island mammal extinctions are determined by interactive effects of life history, island biogeography and mesopredator suppression. *Glob Ecol Biogeogr* 23:395–404.

Heaney LR. 1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia. *Oecologia* 61:11–17.

Henneberg M, Eckhardt RB. 2014. Evolved developmental homeostasis disturbed in LB1 from Flores, Indonesia, denotes Down syndrome and not diagnostic traits of the invalid species *Homo floresiensis*. *PNAS* 111:11967–11972.

Hershkovitz I, Kornreich L, Laron Z, 2007. Comparative skeletal features between *Homo floresiensis* and patients with primary growth hormone insensitivity (Laron Syndrome). *Am J Phys Anthropol* 134:198–208.

Hill KR et al. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331, 1286-1289.

Holliday TW, Franciscus RG. 2009. Body size and its consequences: allometry and the lower limb length of Liang Bua 1 (*Homo floresiensis*). *J Hum Evol* 57:223–228.

Holt RD, Lawton JH, Polis GA, Martinez ND. 1999. Trophic rank and the species-area relationship. *Ecology* 80:1495-504.

Houghton P. 1996. People of the great ocean: aspects of human biology of the early Pacific. New York: Cambridge University Press.

Illius AW, Gordon IJ. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Acta Oecolog. Int J Ecol* 9:428—434

Isbell LA. 2005. Predation on primates: Ecological patterns and evolutionary consequences. *Evol Anthropol* 3: 61–71.

Itescu Y. 2019. Are island-like systems biologically similar to islands? A review of the evidence. *Ecography* 42:1298–1314.

Itescu Y, Schwarz R, Meiri S, Pafilis P. 2017. Intraspecific competition, not predation, drives lizard tail loss on islands. *J Anim Ecol* 86:66–74.

Jaffe AL, Slater GJ, Alfaro ME. 2011. The evolution of island gigantism and body size variation in tortoises and turtles. *Biol Lett* 7:558–561.

Jeschke JM, Kokko H. 2009. The roles of body size and phylogeny in fast and slow life histories. *Evol Ecol* 23:867–878.

Jones JH. 2011. Primates and the evolution of long, slow life histories. *Curr Biol* 21:708–717.

Jordana X, Köhler M. 2011. Enamel microstructure in the fossil bovid *Myotragus balearicus* (Majorca, Spain): Implications for life-history evolution of dwarf mammals in insular ecosystems. *Palaeogeogr Palaeoclimatol Palaeoecol*. 300:59–66.

Jungers WL. 2013. *Homo floresiensis*. A Companion to Paleoanthropology New Jersey: Blackwell Publishing Ltd. pp. 582–598.

Jungers WL, Harcourt-Smith WEH, Wunderlich RE, Tocheri MW, Larson SG, Sutikna T, et al. 2009. The foot of *Homo floresiensis*. *Nature*. 459:81–84.

Jungers WL, Larson SG, Harcourt-Smith W, Morwood MJ, Sutikna T, Due Awe R, et al. 2009. Descriptions of the lower limb skeleton of *Homo floresiensis*. *J Hum Evol* 57:538–554.

- Kaifu Y, Baba H, Sutikna T, Morwood MJ, Kubo D, Saptomo EW, et al. 2011. Craniofacial morphology of *Homo floresiensis*: description, taxonomic affinities, and evolutionary implication. *J Hum Evol* 61:644–682.
- Kaifu Y, Kono RT, Sutikna T, Saptomo EW, Jatmiko, Due Awe R. 2015. Unique Dental Morphology of *Homo floresiensis* and Its Evolutionary Implications. *PLoS One* 10:e0141614.
- Kaifu Y, Kono RT, Sutikna T, Saptomo EW. 2015. Descriptions of the dental remains of *Homo floresiensis*. *Anthro Sci* 150501.
- Kato K, Ogata T. 1989. Main long bones of limbs of the Jomon people: proportions in their lengths. *Okajima's Folia Anatomica Japon* 66, 13-22.
- Kleiber M. 1932. Body size and metabolism. *Hilgarida* 6:315–353.
- Laland K, Matthews B, Feldman MW. 2016. An introduction to niche construction theory. *Evolutionary Ecology* 30:191-202.
- Larson SG, Jungers WL, Morwood MJ, Sutikna T, Jatmiko, Saptomo EW, et al. 2007. *Homo floresiensis* and the evolution of the hominin shoulder. *J Hum Evol* 53:718–731.
- Larson SG, Jungers WL, Tocheri MW, Orr CM, Morwood MJ, Sutikna T, et al. 2009. Descriptions of the upper limb skeleton of *Homo floresiensis*. *J Hum Evol* 57:555–570.
- Lawlor TE. 1982. The Evolution of Body Size in Mammals: Evidence from Insular Populations in Mexico. *Am Nat* 119:54–72.

Lawlor TE. 1986. Comparative biogeography of mammals on islands. Biological Journal of the Linnean Society. pp. 99–125

Leach WN. 2006. Alaskan Eskimo and Polynesian Island population skeletal anatomy: the “Pacific Paradox” revisited through surface area to body mass comparisons. Thesis, University of Montana.

Lewontin RC. 1965. Selection for Colonizing Ability In:“ The Genetic of Colonizing Species”,(Eds.): Baker, HG and Stebbins, Initial. Academic Press, San Diego.

Lomolino MV. 1984a. Immigrant Selection, Predation, and the Distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on Islands. Am Nat 123:468–483.

Lomolino MV. 1984b. Mammalian island biogeography: effects of area, isolation and vagility. Oecologia 61:376–382.

Lomolino MV. 1985. Body Size of Mammals on Islands: The Island Rule Reexamined. Am Nat 125:310–316.

Lomolino MV. 1986. Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. Biological Journal of the Linnean Society 1–21.

Lomolino MV. 1990. The Target Area Hypothesis: The Influence of Island Area on Immigration Rates of Non-Volant Mammals. Oikos 57:297–300.

Lomolino MV. 1994. Species Richness of Mammals Inhabiting Nearshore Archipelagoes: Area, Isolation, and Immigration Filters. J Mammal 75:39–49.

Lomolino MV. 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? J Biogeogr 23:699–703.

Lomolino MV. 2000a. A species-based theory of insular zoogeography. *Glob Ecol Biogeogr* 9:39–58.

Lomolino MV. 2000b. Ecology's most general, yet protean 1 pattern: the species-area relationship. *J Biogeogr* 27:17–26.

Lomolino MV. 2001. The species-area relationship: new challenges for an old pattern. *Prog Phys Geogr* 25: 1–21.

Lomolino MV. 2005. Body size evolution in insular vertebrates: generality of the island rule. *J Biogeogr* 32:1683–1699.

Lomolino MV, Brown JH, Sax DF. 2009. Island biogeography theory. In: Losos JB, Ricklefs RE, editors. *The Theory of Island Biogeography Revisited*. Princeton: Princeton University Press. pp. 13–51.

Lomolino MV, Brown JH. 2009. The Reticulating Phylogeny of Island Biogeography Theory. *Q Rev Biol* 84:357–390.

Lomolino MV, Sax DF, Palombo MR, van der Geer AA. 2012. Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. *J Biogeogr* 39:842–854.

Lomolino MV, Sax DF, Riddle BR, Brown JH. 2006. The island rule and a research agenda for studying ecogeographical patterns. *J Biogeogr* 33:1503–1510.

Lomolino MV, Weiser. 2001. Towards a more general species-area relationship: diversity on all islands, great and small. *J Biogeogr* 28:431–445.

Losos JB. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. American Society of Naturalists E. O. Wilson award address. Am Nat 175:623–639.

Losos JB, Jackman TR, Larson A, Queiroz K, Rodriguez-Schettino L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

Losos JB, Ricklefs RE. 2009. Adaptation and diversification on islands. Nature 457:830–836.

Lyras GA, Dermitzakis MD, Van der Geer AAE, Van der Geer SB, De Vos J. 2009. The origin of *Homo floresiensis* and its relation to evolutionary processes under isolation. Anthropol Sci 117:33–43.

Lyras GA, Van Der Geer AAE, Rook L. 2010. Body size of insular carnivores: evidence from the fossil record: Body size of fossil insular carnivores. J Biogeogr 37:1007–1021.

MacArthur RH, and Wilson EO. 1967. The Theory of Island biogeography. Princeton University Press, Princeton, NJ, USA.

Malinowski B. 1920. Kula; the Circulating Exchange of Valuables in the Archipelagoes of Eastern New Guinea. Royal Anthropological Institute of Great Britain and Ireland. 20:97-105.

Marshall LG, Corruccini RS. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. Paleobiology 1:101-119.

Martin RD, MacLarnon AM, Phillips JL, Dussubieux L, Williams PR, Dobyns WB. 2006. Comment on “The Brain of LB1, *Homo floresiensis*.” Science 312:999.

Masters JC, Génin F, Silvestro D, Lister AM, DelPero M. 2014. The red island and the seven dwarfs: body size reduction in *Cheirogaleidae*. Riddle B, editor. J Biogeogr 41:1833–1847.

Mead M. 1928. Coming of age in Samoa. Penguin Press, New York.

Meiri S. 2007. Size evolution in island lizards. Glob Ecol Biogeogr 16:702–708.

Meiri S. 2008. Evolution and ecology of lizard body sizes. Glob Ecol Biogeogr 17:724–734.

Meiri S, Cooper N, Purvis A. 2008. The island rule: made to be broken? Proc Biol Sci 275:141–148.

Meiri S, Dayan T, Simberloff D. 2005. Area, isolation and body size evolution in insular carnivores. Ecol Lett 8:1211–1217.

Meiri S, Dayan T, Simberloff D. 2004. Body size of insular carnivores: little support for the island rule. Am Nat 163:469–479.

Meiri S, Dayan T, Simberloff D. 2006. The generality of the island rule reexamined. J Biogeogr 33:1571–1577.

Meiri S, Raia P, Phillimore AB. 2011. Slaying dragons: limited evidence for unusual body size evolution on islands. J Biogeogr 38:89–100.

Migliano AB. 2005. Why pygmies are small: ontogenetic implications of life history evolution. PhD dissertation, University of Cambridge.

Migliano AB, et al. 2013. Evolution of the pygmy phenotype: Evidence of positive selection from genome-wide scans in African, Asian, and Melanesian pygmies. *Hum Biol* 85:251–284.

Migliano AB, Vinicius L, Lahr MM. 2007. Life history trade-offs explain the evolution of human pygmies. *PNAS* 104:20216-20219.

Montgomery SH. 2013. Primate brains, the “island rule” and the evolution of *Homo floresiensis*. *J Hum Evol* 65:750–760.

Montgomery SH, Capellini I, Barton RA, Mundy NI. 2010. Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and *Homo floresiensis*. *BMC Biol* 8:9.

Novosolov M, Raia P, Meiri S. 2013. The island syndrome in lizards. *Glob Ecol Biogeogr* 22:184–191.

Orr CM, Tocheri MW, Burnett SE, Awe RD, Sapitomo EW, Sutikna T, et al. 2013. New wrist bones of *Homo floresiensis* from Liang Bua (Flores, Indonesia). *J Hum Evol* 64:109–129.

Pafilis P, Meiri S, Foufopoulos J, Valakos E. 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften* 96:1107–1113.

Palombo MR. 2009. Body size structure of Pleistocene mammalian communities: what support is there for the island rule? *Integr Zool* 4:341–356.

Pélabon C, Bolstad GH, Egset CK, Cheverud JM, Pavlicev M, Rosenqvist G. 2013. On the relationship between ontogenetic and static allometry. *The American Naturalist* 181:195-212.

Perry GH, Dominy NJ. 2009. Evolution of the human pygmy phenotype. *Trends Ecol Evol* 24:218–225.

Price TD, Sol D. 2008. Introduction: genetics of colonizing species. *Am Nat* 172 Suppl 1: S1–3.

Raia P, Meiri S. 2006. The island rule in large mammals: paleontology meets ecology. *Evolution* 60:1731–1742.

Richards GD. 2006. Genetic, physiologic and ecogeographic factors contributing to variation in *Homo sapiens*: *Homo floresiensis* reconsidered. *J Evol Biol* 19:1744–1767.

Roth VL. 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. *Oxford Surveys in Evo Bio* 8:259.

Rozzi FVR, Koudou Y, Froment A, Le Bouc Y, Botton J. 2015. Growth pattern from birth to adulthood in African pygmies of known age. *Nat Comm* 6:7672.

Ruff C. 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearb Phys Anthropol* 37:65-107.

Ruff C. 2002. Variation in human body size and shape. *Annual Review of Anthropology* 31:211-232.

Runemark A, Sagonas K, Svensson EI. 2015. Ecological explanations to island gigantism: dietary niche divergence, predation, and size in an endemic lizard. *Ecology* 96:2077–2092.

- Schillaci MA, Meijaard E, Clark T. 2009. The effect of island area on body size in a primate species from the Sunda Shelf Islands. *J Biogeogr* 36:362–371.
- Sondaar PY. 1977. Insularity and its effect on mammal evolution. Pages 671-707 in P. C. Goody, B. M. Hecht, and M. K. Hechtieds, eds. *Major patterns of vertebrate evolution*. Plenum, New York.
- Sondaar PA, Boekschoten GJ. 1967. Quaternary mammals in the south Aegean Islands Arc, I & II. *Proc. Kon. Ned. Akad. Wetensch. Amsterdam B* 70:556–576.
- Stearns SC. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41:173–187.
- Stearns SC. 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87:476–486.
- Stone JH, Fitzpatrick SM, Napolitano MF. 2017. Disproving claims for small-bodied humans in the Palauan archipelago. *Antiquity* 91:1546–1560.
- Sutikna T, Tocheri MW, Morwood MJ, Sapomo EW, Jatmiko, Awe RD, et al. 2016. Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. *Nature* 532:366–369.
- Temple DH, Matsumura H. 2011. Do body proportions among Jomon foragers from Hokkaido conform to ecogeographic expectations? Evolutionary implications of body size and shape among northerly hunter-gatherers. *Int J Osteoarchaeol* 21:268–282.
- Templeton AR. 1980. The theory of speciation via the founder principle. *Genetics* 94:1011–1038.

Tocheri MW, Orr CM, Larson SG, Sutikna T, Jatmiko, Sapomo EW, et al. 2007. The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. *Science* 317:1743–1745.

van der Geer AAE. 2014. Parallel patterns and trends in functional structures in extinct island mammals. *Integr Zool* 9:167–182.

van der Geer AAE, Lyras GA, De Vos J, Dermitzakis M. 2011. Evolution of island mammals: adaptation and extinction of placental mammals on islands.

van der Geer AAE, Lyras GA, Drinia H. 2013a. Trends of body size evolution in the fossil record of insular Southeast Asia. Sage 11.

van der Geer AAE, Lyras GA, Lomolino MV. 2013b. Body size evolution of palaeo-insular mammals: temporal variations and interspecific interactions. *J Biogeogr* 40:1440–1450.

van der Geer AAE, Lyras GA, MacPhee RDE, Lomolino M, Drinia H. 2014. Mortality in a Predator-free Insular Environment: the Dwarf Deer of Crete. *American Museum Novitates* 3807:1–26.

van Heteren AH. 2008. *Homo floresiensis* an Island form. *J Vertebr Paleontol* 5:1–12.

Van Valen L. 1973. Pattern and the balance of nature. *Evol Theory* 1:31–49.

Veatch EG, Ringen EJ, Kilgore MB, Jatmiko. 2021. Using niche construction theory to generate testable foraging hypotheses at Liang Bua. *Evol Anthropol* 30:8–16.

Veatch EG, Tocheri MW, Sutikna T, McGrath K, Wahyu Sapomo E, Jatmiko, et al. 2019. Temporal shifts in the distribution of murine rodent body size classes at

Liang Bua (Flores, Indonesia) reveal new insights into the paleoecology of *Homo floresiensis* and associated fauna. J Hum Evol 130:45–60.

Wallace AW. 1880. Island Life. University of Chicago Press, USA.

Weissner P et al. 2002. The vines of complexity: egalitarian structures and the institutionalization of inequality among Enga. Curr Anthropol 43:233-269.

West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. Science 276.

Weston EM, Lister AM. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. Nature 459:85–88.

White JF, Gould SJ. 1965. Interpretation of the coefficient in the allometric equation. The Am Nat 99:5-18.

Yamaguchi B. 1989. A review of the osteological characteristics of the Jomon population in prehistoric Japan. J Anthropol Soc Nip 90:77-90.

Young CB. 2020. Static allometry of a small-bodied omnivore: body size and limb scaling of an island fox and inferences for *Homo floresiensis*. J Hum Evo 147.

## **CHAPTER 2:**

### **PRIMATE BODY SIZE DIVERSITY ON ISLANDS AND IMPLICATIONS FOR THE ISLAND RULE**

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#### **Abstract**

Primates exhibit remarkable geographic success and phenotypic variation in diverse island settings, yet how the island rule applies to them is poorly understood. To better describe primate body sizes on islands, I explored the effect that area has on primate body mass on islands near Africa and Asia. I interpret these results in light of the evolutionary history of primates and the novel evolutionary processes on islands and provide a new perspective for describing primate body size diversity on islands. Within the Order Primates, area has a slightly negative effect on body mass; larger islands contain a greater proportion of smaller-bodied (<2700 g) primates. Larger-bodied primates (>2700 g) are more abundant and evenly distributed across all island areas, including smaller areas. However, when small and large primates were analyzed separately, area does not covary with body mass within each group. Periods of isolation subsequent to sea level rise in Southeast Asia favored extinction of smaller body sizes on more islands overall. Prolonged isolated on larger islands, though, favored speciation events of smaller bodied species. These results support the idea that the island rule does

not describe body sizes evolving in response to limited area, directly, but instead describes how differential selective pressures on island ecologies influence body size for a particular taxon.

**Key words:** Island biogeography, primates, body size, island rule, island evolution

## Introduction

Organisms often evolve divergent phenotypes in island areas. In many instances, when organisms migrate to and colonize an island body size alterations occur. The presence of altered body sizes on islands is so common that an ecological rule was developed (Van Valen, 1973). Known as “the island rule”, generally large-bodied organisms get smaller and small-bodied organisms get larger on a cline that is related to the original body size of the organism (Foster, 1964; Van Valen, 1973; Lomolino, 1985, 2005). While body size alterations are apparent in many mammals such as proboscideans, artiodactyls, rodents, and lagomorphs, how primates alter body sizes in response to island areas is less understood. Here, I identify the relationship between island area and primate body size distribution in a large sample of primates ( $N=221$ ) to test how area influences body size of primates on islands near Africa and Asia. I interpret these results in light of the evolutionary history of primate body sizes in the mainland.

Body size is intimately connected to the dietary and reproductive strategies of an organism. On islands with reduced predation and community members around finite resources, selective pressures to maintain larger body size may not be present. Smaller

size evolves for its ability to outcompete other population members for finite resources after this ecological release (Lomolino et al., 2012). Body size reduction (dwarfism) on islands that follows this pattern is common in hippos, elephants, and deer (Sondaar, 1977; van der Geer et al., 2011, 2013; Athanassiou et al., 2019). Degree of dwarfism in these organisms tends to covary with area, not due to limited resources, but likely due to changes in competitors and predators (Athanassiou et al., 2019). Island areas that contain fewer competitors, such as smaller ones, influence body size evolution in these organisms more drastically (Palombo, 2009; van der Geer et al., 2016). Small-bodied organisms, such as rodents, tend to get larger also a response to predator and competitor relaxation following migration to an area (Foster, 1963, 1964; Freudenthal, 1972; Magnanou et al., 2005). Introduction to the selective pressures of migrating over a boundary paired with the absence of the selective pressures shaping small body size in the mainland (such as predators) in the colonized island area play the most significant roles in determining enlargement of small species (Lomolino et al., 2012, 2013).

Therefore, body size alterations to differential selective pressures of islands relate to the dietary and reproductive role a body size played in the mainland and the subsequent selective pressures of the island (Raia and Meiri, 2006; Lyras et al., 2010; Lomolino et al., 2012; Baiser et al., 2019). The island rule is likely not a direct response to decreased nutrition (such as daily caloric intake), but a phenomenon that is highly context specific and relates to the evolved body size of the mainland organism and subsequent island ecological interactions. In many organisms there is little evidence for body size relating directly to island area (Meiri et al., 2004, 2005, 2006, 2008; van der Geer et al., 2018). For instance, carnivore body size alterations are not directly related to

island area but the size of available prey species (van der Geer et al., 2018). Carnivores on islands may adjust body size in response to available prey species as seen, for example, in the reduced limbs and skeletal size of the canid *Cynotherium sardous* in response to smaller sized prey (Lyras and van der Geer, 2006).

Primates display remarkable variation in body size and often inhabit islands. But research has yet to conclusively agree regarding whether primates follow the island rule (Bromham and Cardillo, 2007; Meiri et al., 2008; Schillaci et al., 2009; Weston and Lister, 2009; Welch, 2009; Baab, 2012; Montgomery, 2013). This research became increasingly debated within anthropology subsequent to the discovery of a small-bodied hominin, *Homo floresiensis* (Brown et al., 2004), on the island of Flores, Indonesia. Late Pleistocene (100-60 kya; Sutikna et al., 2016) fossils indicate that this island hominin displayed an extraordinary small stature (106 cm; Brown et al., 2004) with a disproportionately small relative brain size and unique cranial traits and limb proportions compared to any extant or extinct hominin (Aiello, 2010). Research to explore if this small-bodied hominin is the result of adapting to and surviving in an island ecology has tested whether primates demonstrate body size reduction in various island areas and have conflicting results likely due to differences in sampling and theoretical design (Bromham and Cardillo, 2007; Welch, 2009; Schillaci et al., 2009; Montgomery, 2013).

Bromham and Cardillo (2007) and Welch (2009) analyzed roughly 30 species of island and mainland primates that were selectively sampled due to pre-established differences between the island and mainland pairs, and both found that the island species had smaller body masses compared to the mainland counterparts. Montgomery (2013) analyzed seven select island and mainland pairs and found similar results for body mass,

but not brain mass. However, work by Schillaci et al. (2009) using long-tailed macaques (*Macaca fascicularis*) concluded that island area does not covary with body or skull length in these primates, such that smaller island areas do not contain smaller macaques, and therefore primates do not follow the island rule. These results are not necessarily contradictory, because the island rule does not state that organismal size is correlated to island area, rather, body size responses to islands are the result of ecological release and shifting selective pressures.

### *Primate body size diversity on islands*

While some research has suggested that mainland primate body size is an evolved response to predation pressures (Anderson, 1986; Isbell, 2005), primates likely didn't evolve a body size for predator defense. Instead, primates likely evaded predators by adapting to an arboreal, frugivorous niche with altered biological and behavioral traits (Boinski & Chapman, 2005; Sussman et al., 2013). Primates have relatively slow life histories with elongated reproductive periods compared to other mammals of similar body masses (Austad and Fischer, 1992; Charnov and Berrigan, 1993; Judge and Carey, 2000; Shattuck and Williams, 2010). Jones (2011) interpreted this as an evolved response to unpredictable environments, due to an ancestral dietary niche of eating high quality, nutrient dense food such as fruit that is particularly temperamental and seasonal. A life history strategy that supported current somatic survival to reduce adult mortality and expand reproductive effort over multiple years likely increased fitness in this dietary niche (Blomquist, 2009; Jones, 2011). As body size alterations are also related to life

history adjustments, primate body size adjustments on islands may be related to life history adjustments in response to novel island resources (Ross, 1998).

To better understand how primate diversity is influenced by island areas, a broad analysis that assesses how area influences species abundance and body sizes for primates across various island areas is necessary. With over 200 species on diverse islands (from 15 km<sup>2</sup> to as large as 743,330 km<sup>2</sup>) primates exhibit remarkable variation in body size (30 g to 100,000 g). Further, primate species abundance on islands is mostly the result of vicariance, not immigration, showing a lack of correlation with distance of the island from the mainland (Harcourt, 1999). Therefore, area, and the differential community-resource dynamics therein, should influence patterns of species diversity that reflect survival within islands. Over time, extinction rates in these isolated areas will have produced the distribution of body sizes present in these regions (MacArthur and Wilson, 1967). To explore this matter, I assess how body masses covary with area for primates on islands adjacent to Africa and Asia. Identifying how body masses are patterned for primates over diverse island areas may further illuminate the factors that have driven diversity in primates worldwide. Further, it will inform interpretations of the island rule and how body size alterations on islands depends on the evolved characteristics of the mainland organism and subsequent responses to island ecologies.

To demonstrate how primates that likely evolved body sizes to increase survival within a mainland frugivorous niche respond to the unique pressures of island ecologies, I assessed how body masses contribute to species abundance of primates on islands near Africa and Asia. First, does body mass of these primates covary with island area? Second, do small-bodied primates increase in size on smaller islands? And do large-

bodied primates decrease in size on smaller islands? Last, in what island areas are small and large body sizes favored?

## Methods

### *Sample*

To assess patterns of body mass of primate species on islands of different areas, I gathered data on 221 primate species on 35 islands using the IUCN RedList (IUCN, 2021). I compiled island area using google maps as km<sup>2</sup>. Island area was defined as the extension of terrain per island, not per archipelago (Table 1). To assess how body masses are patterned for these species on island areas, average female body mass in grams per taxon per island was gathered using the literature (Smith and Jungers, 1996; PIN, 2021).

## Analysis

To identify how body mass covaries with area and is distributed among these primate species, three ordinary least squares linear regressions were constructed to identify the relationship between logged area (km<sup>2</sup>) on the x axis and logged body mass (g) on the y axis with 95% confidence intervals for all taxa, and small- (<2700 g), and large-bodied (>2700 g) primates. Primates were divided into small (<2700 g) and large (>2700 g) body mass categories based on previously reported extinction thresholds for mammals on islands (Hanna and Cardillo, 2014). Lastly, frequency distributions of number of islands occupied by primates within each size category were constructed using Fisher's log-series to assess the overall distribution of body sizes among island areas.

Fisher's log-series is a biodiversity index that signifies the relative richness and equitability of taxa for a habitat, where the higher alpha index communicates greater contributions of both richness and equitability and therefore greater biodiversity. A lower alpha index indicates richness, equitability, or both are reduced, contributing to less biodiversity. Therefore, it is a relative index and best used when comparing among samples of interest. Here, I use the Fisher's log-series to compare how small- (<2700 g) and large-bodied primates (>2700 g) differ in richness and equitability across islands. The body mass category with a higher alpha index will signify greater abundance (richness) and evenness (equitability) across islands, demonstrating greater success of this reproductive strategy in a wider variety of islands.

## Results

Results of the linear regression of logged body mass (g) distributed by logged area ( $\text{km}^2$ ) of these species indicate that there is a slight ( $r^2=0.05$ ) but significant ( $p<0.001$ ) effect of area on body mass (Figure 1). As island area increases, body size slightly decreases. When small- ( $N=121$ ) and large-bodied ( $N=128$ ) primates are analyzed separately against area, the effect disappears (Figure 2 and 3). While there is a slight ( $r^2=0.03$ ) positive relationship between body mass and area for small primates, this does not reach significance (Figure 2). Further, large primates do not show a significant relationship between island area and body mass (Figure 3). Small-bodied primates do not get larger on smaller islands, and large-bodied primates do not get smaller on smaller islands.

Results of the Fisher log-series biodiversity test comparing body mass of primates across islands indicates that large-bodied primates ( $N=128$ ) have a higher alpha index than small-bodied primates ( $N=121$ ) with  $\alpha=25.91$  and  $5.26$ , respectively. Relative frequency distributions of small- and large-bodied primates are depicted in Figure 4, and Table 2 summarizes the number of taxa in each size category and the number of islands these sizes occupy. Smaller-bodied primates are more abundant on fewer islands, concentrating on the largest islands such as Madagascar, Borneo, and Sumatra. Larger-bodied taxa are more abundant on smaller islands and occur more evenly and frequently across islands.

## **Discussion**

While it is preferred to compare the degree of body size alterations in relation to closely related mainland ancestors, many island primate taxa do not have clear mainland comparisons. Future genomic and paleontological work are necessary to elucidate mainland and ancestral body forms of many island primates prior to isolation. The work presented here is a necessary starting point to begin to discuss how primate body sizes evolve and respond to different island areas. The purpose of this research was to provide a new perspective on how island areas influence primate diversity with special attention on explaining body size evolution of primates. In doing so, I described how primate body sizes evolved within a frugivorous niche, related to life history alterations to survive within this niche. I then identified how primate body masses are patterned among island areas adjacent to Africa and Asia to understand how area influences primate diversity.

Last, I assessed how small and large body sizes covary with island areas to test whether the presence of primate body sizes is broadly related to island area.

Analyses of body masses of all primate taxa indicate that island area has a slightly negative but significant effect on body mass, such that smaller species are more abundant on larger islands suggesting that resource-rich and highly competitive arboreal environments favor small-bodied primates. These results support Heaney's (1978) predictions for insular mammals based off analyses of squirrels in Southeast Asia. Heaney (1978) predicted that small body sizes may be selected for in large island areas with intense competition around finite resources due to increased intraspecific competition among community members. The high concentration of small-bodied primates on large, highly competitive environments, is also supported by Fisher's log series (Figure 4).

Smaller body size is less abundant overall, though, suggesting high extinction rates of small-bodied primate taxa among more island areas. These results contradict predictions by MacArthur and Wilson (1967) that suggested fast life histories, and therefore smaller body sizes, would be a more successful colonizing strategy overall. For primates, smaller body sizes, and associated quicker reproduction, in primates may be more successful in resource rich, larger environments, and outcompete delayed reproduction. Larger body sizes with elongated life histories may support survival in unpredictable environments, such as small island areas, more so than smaller body sizes. Large primates on islands are mostly comprised of cercopithecoids ( $N=85$ ) with a high abundance of *Macaca* ( $N=27$ ) and *Presbytis* ( $N=25$ ) who occupy diverse island areas as small as  $15 \text{ km}^2$  (Perhentian) and as large as  $743,330 \text{ km}^2$  (Borneo). Smaller areas with

decreased resources may support primates able to invest in current somatic maintenance and delay reproduction more so than fast producing primates. Large body sizes with elongated life histories are more abundant overall and successful in smaller island areas with high seasonal resource scarcity and unpredictability.

High levels of competition among arboreal primates driving smaller body size is further exemplified by lemurs on Madagascar. While large (592,800 km<sup>2</sup>), Madagascar is still considered an island as it has been separated from continental landmasses for at least 85 million years, prior to the terminal Cretaceous mass extinction event that wiped species from Madagascar about 65 million years ago (Rabinowitz et al., 1983). Initial colonization by primates required migrating over the Mozambique Channel and included colonizing a species-depauperate, isolated landmass. Therefore, despite being large, the long-term separation of this landmass during early primate evolution coupled with the migratory colonization by lemuriform ancestors supports distinct island evolutionary processes being present compared to the nearby mainland.

Madagascar is home to over a hundred lemuriforms, which are small-bodied primates with fast generation times and high reproductive rates (*Varecia varecia* has one of the highest values among primates; Ross, 1998). Lemuriforms represent an adaptive radiation event that was probably fostered by the large and diverse habitat area, lack of species during initial colonization, and reproductive success of the taxa (Martin, 1972). Of the N=111 lemuriforms that inhabit Madagascar, N=92 were categorized as small while N=19 were large. Fossil evidence of subfossil lemurs indicate some gigantism (giant lemurs, e.g. *Megaladapis* and *Palaeopropithecus*; Godfrey et al., 1997), possibly related to the processes of migrating to and colonizing a predator-depauperate

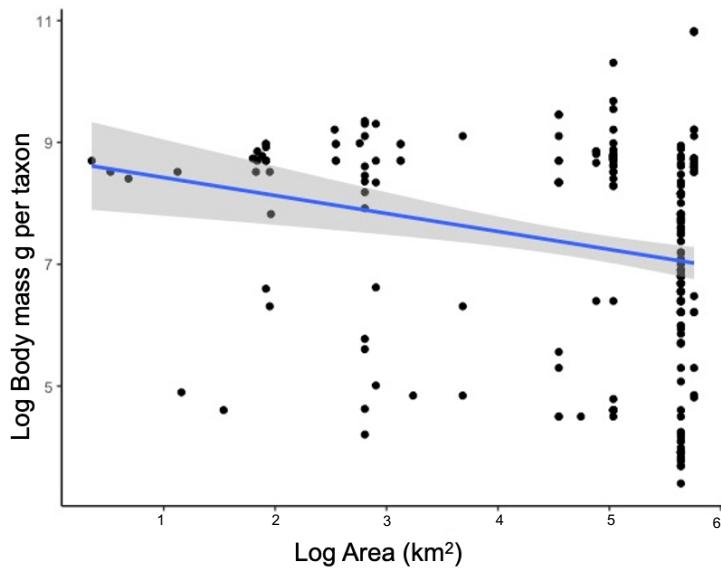
environment, similar to other small-bodied taxa such as rodents (Lomolino et al., 2012). However, recent extinction of large lemuriforms may be related to increased community competition among primate species (including humans) driving larger body sizes out of this region over longer periods of time. Having a smaller body size, with faster development, and higher reproductive rates was favored in this larger environment with increased resources and community competition. Primates with higher reproductive rates and faster life histories may have increased fitness advantage in larger island areas with increased resource abundance and competition and may in fact demonstrate phyletic dwarfs (Masters et al., 2014).

Further, primate genera have evolved diverse feeding and behavioral adaptations that may require a more refined analysis to assess how body sizes respond to islands. For instance, tarsiers are small-bodied carnivorous primates that likely do not increase in size on small islands because their prey on these islands are also small. Further, as primates have increased cognitive and social complexity compared to other mammals, these learned behavioral traits may act to reduce intraspecific competition among finite resources in these areas. Macaques in Siberut (*Macaca siberut*) demonstrate altered behaviors, such as greater foraging distances, in response to decreased tree richness compared to mainland macaques (*M. nemestrina*; Richter et al., 2013). Long-tailed macaques *M. fascicularis* spp. on Piak nam Yai and Nicobar Islands also use stones and other materials to forage and crack open shellfish and crabs (Malaivijitnond et al., 2007; Pal et al., 2017). An analyses that contextualizes these body sizes with their unique evolutionary histories and the responses to differential island areas may be more fruitful than simply comparing to other herbivores on islands

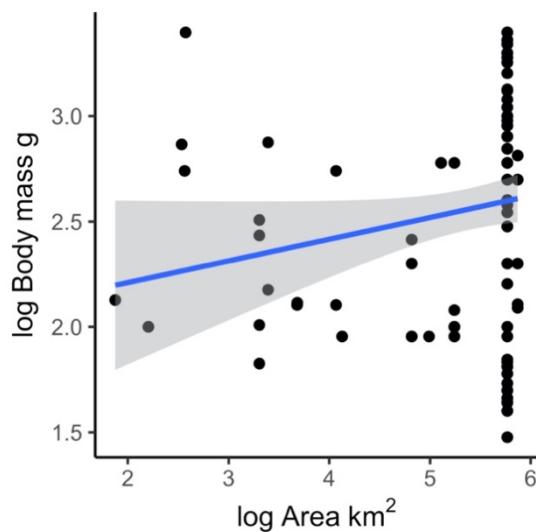
These results add to growing research on the island rule that indicates body size alterations are not directly related to island area but relate to how a specific organism responds to alterations in selective pressures on islands (Raia and Meiri, 2006; Lomolino et al., 2012, 2013). Body size reduction in island areas is likely not a direct response to resource availability, but a dynamic interplay among the evolutionary niche of an organism and the subsequent community-resource dynamics of an island area. Similar to strict carnivores, primate body sizes may not be impacted by lack of predation on islands, such that body size does not covary with island area, but other aspects of island ecology (Meiri et al., 2005). Organisms respond to the effects of island area in diverse ways and primates who evolved to maintain high fitness via elongated life histories in unpredictable mainland environments likely alter body size on islands after being released from these pressures and introduced to novel island ones, such as increased competition among arboreal species in a resource rich environment.

### **Acknowledgements**

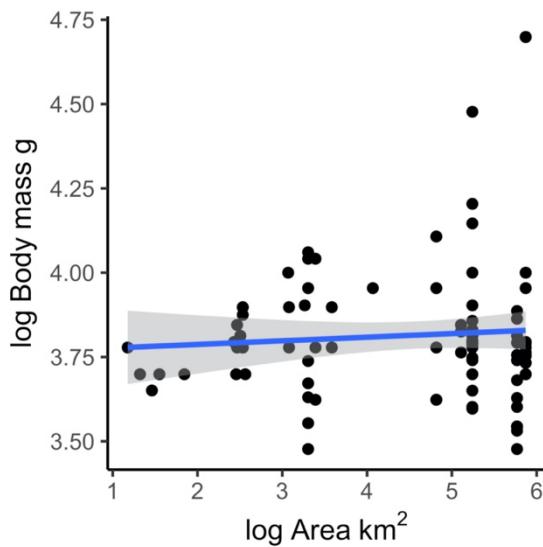
This work was supported by the National Science Foundation Graduate Research Fellowship Program grant no. DGE-1443129. Special thanks to helpful discussions and comments on drafts by Agustín Fuentes, Karthik Panchanathan, Matthew Gompper, and Libby Cowgill.



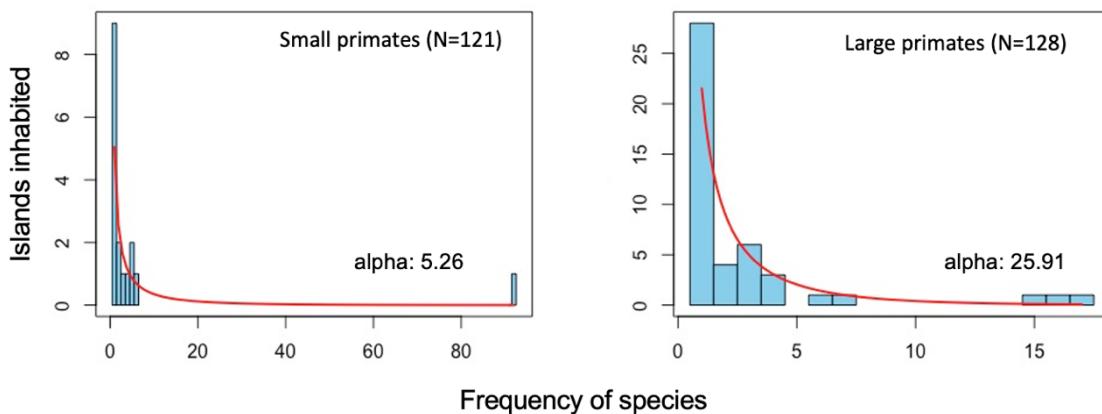
**Figure 2.1:** OLS regression ( $y = \alpha + \beta x$ ) of log(body mass g) distributed by log(area km<sup>2</sup>) of primates on islands near Africa and Asia:  $\alpha = 9.01$ ,  $\beta = -0.15$ ,  $r^2 = 0.05$ , p-value=<0.001. Grey=95% CI of mean.



**Figure 2.2:** Small-bodied (<2700 g) primates on islands near Africa and Asia OLS regression ( $y = \alpha + \beta x$ ) of log(body mass g) distributed by log(area km<sup>2</sup>):  $\alpha = 2.01$ ,  $\beta = 0.10$ ,  $r^2 = 0.03$ , p-value=0.07. Grey=95% CI of mean.



**Figure 2.3: Large-bodied (>2700 g) primates on islands near Africa and Asia OLS regression ( $y = \alpha + \beta x$ ) of log(body mass g) distributed by log(area km<sup>2</sup>):  $\alpha = 3.77$ ,  $\beta = 0.01$ ,  $r^2 = 0.004$ , p-value = 0.48. Grey = 95% CI of mean.**



**Figure 2.4: Fisher's log-series frequency test for richness and equitability of small and large primates across islands near Africa and Asia.**

**Table 2.1: Island location and associated species-area components for N=221 primates.**

<b>Island</b>	<b>Area km<sup>2</sup></b>	<b>Species</b>
Perhentian	15	1
Khram Yai	21	1
Con son	29	1
Maratua	36	1
Karimunjawa	70	1
Serasen	75	1
Siau	160	1
Sipora	245	4
Karimata	270	2
Tarutao	286	2
Phenang	293	2
Langkawi	320	1
North Pagai	342	4
Bongao	366	2
Mayotte	374	1
Pemba	988	5
Bintang	1173	1
South Pagai	1200	4
Nicobar*	1841	2
Bioko	2017	12
Unguja	2462	5
Siberut	3838	4
Belitung	4801	1
Bohol*	4821	1
Bangka	11693	2
Samar	13428	1
Palawan	14649	1
Sri Lanka	65610	13
Mindanao	97530	2
Java	128297	6
Sulawesi	174600	14
Sumatra	473481	20
Madagascar	587041	111
Borneo	743330	50

**Table 2.2: Abundance and distribution of  
small and large primate body sizes of  
N=221 primates across n=34 islands.**

<b>Body mass</b>	<b>Species (N)</b>	<b>Islands (N)</b>
Small (<2700 g)	121	18
Large (>2700 g)	128	28

## Literature Cited

- Aiello LC. 2010. Five years of *Homo floresiensis*. *Am J Phys Anth* 142:167–179.
- Anderson CM. 1986. Predation and primate evolution. *Am J Primatol* 27:15–39.
- Athanassiou A, van der Geer AAE, Lyras GA. 2019. Pleistocene insular Proboscidea of the Eastern Mediterranean: A review and update. *Quaternary Sci Rev* 218:306–321.
- Austad SN, Fischer KE. 1992. Primate longevity: Its place in the mammalian scheme. *Am J Primatol* 28:251–261.
- Baiser B, Gravel D, Cirtwill AR, Dunne JA, Fahimipour AK, Gilarranz LJ, Grochow JA, Li D, Martinez ND, McGrew A, Poisot T. 2019. Ecogeographical rules and the macroecology of food webs. *Global Ecol Biogeogr* 28:1204-1218.
- Blomquist GE. 2009. Trade-off between age of first reproduction and survival in a female primate. *Biol Letters* 5:339–342.
- Boinski S, Chapman CA. 2005. Predation on primates: Where are we and what's next? *Evol Anth* 4:1–3.
- Bromham L, Cardillo M. 2007. Primates follow the “island rule”: implications for interpreting *Homo floresiensis*. *Biol Letters* 3:398–400.
- Brown P, Sutikna T, Morwood MJ, Soejono RP, Sapomo EW, & Due RA. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055-1061.
- Charnov EL, Berrigan D. 1993. Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evol Anth* 1:191-194.
- Foster J. 1964. Evolution of Mammals on Islands. *Nature* 202:234–235.

- Godfrey LR, Jungers WL, Burney DA. 2010. Subfossil lemurs of Madagascar. *Cenozoic Mammals of Africa*, 351–367.
- Gould S.J. 1977. *Ontogeny and phylogeny*. Belknap Press, Cambridge, MA.
- Hanna E, Cardillo M. 2014. Island mammal extinctions are determined by interactive effects of life history, island biogeography and mesopredator suppression. *Global Ecol Biogeogr* 23:395–404.
- Harcourt AH. 1999. Biogeographic Relationships of Primates on South-East Asian Islands. *Global Ecol Biogeogr* 8:55–61.
- Heaney LR. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Int J Org Evol* 32: 29–44.
- Isbell LA. 2005. Predation on primates: ecological patterns and evolutionary consequences. *Evol Anth* 3:61–71.
- Jones JH. 2011. Primates and the evolution of long, slow life histories. *Curr Biol* 21: R708–R717.
- Judge DS, Carey JR. 2000. Postreproductive life predicted by primate patterns. *J Gerontol A-Biol* 55, B201-B209
- Lomolino MV. 1985. Body size of mammals on islands: the island rule reexamined. *Am Nat* 125:310–316.
- Lomolino MV, Sax DF, Palombo MR, van der Geer AA. 2012. Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. *J Biogeogr* 39:842–854.
- Lomolino MV, van der Geer AA, Lyras GA, Palombo MR, Sax DF, Rozzi R. 2013. Of mice and mammoths: generality and antiquity of the island rule. *J Biogeogr* 40:1427–1439.

- Lyras G, van der Geer A. 2006. Adaptations of the Pleistocene island canid *Cynotherium sardous* (Sardinia, Italy) for hunting small prey. *Cranium* 23:51–60.
- Lyras GA, van der Geer AA, Rook L. 2010. Body size of insular carnivores: evidence from the fossil record: Body size of fossil insular carnivores. *J Biogeogr* 37:1007–1021.
- MacArthur R, Wilson EO. 1967. The theory of island biogeography. Princeton University Press, Princeton, editors: McCoy NJ, Connor EF.
- Magnanou E, Fons R, Blondel J, Morand S. 2005. Energy expenditure in *Crocidurinae* shrews (Insectivora): is metabolism a key component of the insular syndrome? *Comparative Biochemistry and Physiology. Part A, Ann Ny Acad Sci* 142:276–285.
- Martin RD. 1972. Adaptive radiation and behaviour of the Malagasy lemurs. *Philos T Roy Soc B* 264:295–352.
- Masters JC, Génin F, Silvestro D, Lister AM, DelPero M. 2014. The red island and the seven dwarfs: body size reduction in Cheirogaleidae. *J Biogeogr* 41:1833–1847.
- Meiri S, Dayan T, Simberloff D. 2004. Body size of insular carnivores: little support for the island rule. *Am Nat* 163:469–479.
- Meiri S, Dayan T, Simberloff D. 2005a. Area, isolation and body size evolution in insular carnivores. *Ecol Lett* 8:1211–1217.
- Meiri S, Simberloff D, Dayan T. 2005b. Insular carnivore biogeography: island area and mammalian optimal body size. *Am Nat* 165:505–514.
- Meiri S, Dayan T, Simberloff D. 2006. The generality of the island rule reexamined. *J Biogeogr* 33:1571–1577.
- Meiri S, Cooper N, Purvis A. 2008. The island rule: made to be broken? *P R Soc B* 275:141–148.

- Meiri S, Raia P, Phillimore AB. 2011. Slaying dragons: limited evidence for unusual body size evolution on islands. *J Biogeogr* 38:89–100.
- Montgomery SH. 2013. Primate brains, the “island rule” and the evolution of *Homo floresiensis*. *J Hum Evo* 65:750–760.
- Palombo MR. 2009. Body size structure of Pleistocene mammalian communities: what support is there for the island rule. *Integr Zool* 4:341–356.
- PIN, 2021. Primate information network. [www.primate.wis.edu](http://www.primate.wis.edu)
- Rabinowitz PD, Coffin MF, Falvey D. 1983. The separation of Madagascar and Africa. *Science* 220:67–69.
- Raia P, Meiri S. 2006. The island rule in large mammals: paleontology meets ecology. *Int J Org Evol* 60:1731–1742.
- Ross C. 1998. Primate life histories. *Evol Anth* 6:54-63.
- Schillaci MA, Meijaard E, Clark T. 2009. The effect of island area on body size in a primate species from the Sunda Shelf Islands. *J Biogeogr* 36:362–371.
- Shattuck MR, Williams SA. 2010. Arboreality has allowed for the evolution of increased longevity in mammals. *PNAS USA* 107:4635-4639.
- Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *J Hum Evo* 32:523–559.
- Sondaar PY. 1977. Insularity and Its Effect on Mammal Evolution. In M. K. Hecht, P. C. Goody, & B. M. Hecht (Eds.), *Major Patterns in Vertebrate Evolution* pp. 671–707, Springer US.
- Sussman RW, Tab Rasmussen D, Raven PH. 2013. Rethinking primate origins again. *Am J Primatol* 75:95–106.

Sutikna T, Tocheri MW, Morwood MJ, Saptomo EW, Jatmiko Awe RD, Wasisto S, Westaway KE, Aubert M, Li B, Zhao J-X, Storey M, Alloway BV, Morley MW, Meijer HJM, van den Bergh GD, Grün R, Dosseto A, Brumm A, Roberts RG. 2016. Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. *Nature* 532:366–369.

van der Geer AAE, Lyras G, De Vos J, Dermitzakis M. 2011. Evolution of island mammals: adaptation and extinction of placental mammals on islands. John Wiley & Sons.

van der Geer AAE, Lyras GA, Lomolino MV. 2013. Body size evolution of palaeo-insular mammals: temporal variations and interspecific interactions. *J Biogeogr* 40:1440–1450.

van der Geer AAE, Lyras GA, Volmer R. 2018. Insular dwarfism in canids on Java (Indonesia) and its implication for the environment of *Homo erectus* during the Early and earliest Middle Pleistocene. *Palaeogeogr Palaeocl* 507:168–179.

Van Valen L. 1973. Pattern and balance of nature. *Evol Theor* 1:31–49.

Welch JJ. 2009. Testing the island rule: primates as a case study. *Proc Soc R B* 276:675–682.

Weston EM, Lister AM. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature* 459:85–88.

**CHAPTER 3:**

**STATIC ALLOMETRY OF A SMALL-BODIED OMNIVORE: BODY  
SIZE AND LIMB SCALING OF AN ISLAND FOX AND  
INFERENCES FOR *HOMO FLORESIENSIS***

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**Abstract**

Island dwarfing is a paraphyletic adaptation across numerus mammalian genera. From mammoths to foxes, extreme body size reduction is shared by diverse organisms who migrate to an island environment. Because it largely occurs due to ecological variables, not phylogenetic ones, skeletal characters in a dwarfed taxon compared to its ancestor may appear abnormal. As a result, allometric patterns between body size and morphological traits may differ for an island dwarf compared to its ancestor. The diminutive Late Pleistocene hominin, *Homo floresiensis*, displays a unique character suite that is outside of the normal range of variation for any extinct or extant hominin species. To better explain these as ecological traits due to island dwarfing, this research looks at how dwarfing on islands influences limb scaling and proportions in an organism in a similar ecological niche as *H. floresiensis*. Here I analyze absolute limb lengths and static allometry of limb lengths regressed on predicted body mass of dwarfed island foxes and their non-dwarfed relatives. Dwarfed island foxes have significantly smaller intercepts but steeper slopes of all limb elements regressed on predicted body mass compared to the mainland gray fox. These allometric alterations produce limbs in the island fox that are

significantly shorter than predicted for a non-dwarfed gray fox of similar body mass. Additionally, the humerofemoral, intermembral, and brachial indices are significantly different. These results provide a novel model for understanding skeletal variation of island endemic forms. Unique body size and proportions of *Homo floresiensis* are plausible as ecological adaptations and likely not examples of symplesiomorphies with *Australopithecus* sp. Caution should be exerted when comparing an island dwarf to a closely-related species as deviations from allometric expectations may be common.

## Introduction

*Homo floresiensis* is a small-bodied Late Pleistocene island hominin which exhibits a mosaic of unique traits (Aiello, 2010; Brown et al., 2004). Many of these traits are used to support the argument that *H. floresiensis* is phylogenetically closely related to an early hominin species, or even a pathological form of a later hominin. Traits of *H. floresiensis* that appear in early hominin species include: low humeral torsion, primitive wrist and pedal morphology, high intermembral and humerofemoral index, and small brain size (Brown & Maeda, 2009; Jungers et al., 2009a,b; Larson et al., 2006; Schoenemann and Allen, 2006; Tocheri et al., 2007). The presence of an orthognathic face and a vertical forehead have prompted some to argue for a modern human classification, and the small relative brain size as the result of a pathology such as Down Syndrome, microcephaly, or Laron Syndrome (Henneberg, 2014; Hershkovitz et al., 2007; Martin et al., 2006; Richards, 2006). In support of an alternative hypothesis, research on cranial size and scaling, and morphometrics shows that the diminutive brain size and shape more plausibly belong to a *Homo erectus* population who adapted to an island environment via

dwarfing (Argue et al. 2006; Bromham & Cardillo, 2007; Gordon et al., 2008; Kaifu et al., 2011; Lyras et al., 2009; Montgomery et al., 2010; Weston & Lister, 2009). Lack of knowledge on how skeletal traits vary in island dwarf populations makes it difficult to resolve this debate.

Late Pleistocene hominin limb bones from the island of Flores at Liang Bua dating to 100–60 kya ago (Sutikna et al., 2016) display proportions that characterize Late Pliocene early *Australopithecus* sp. Early *Australopithecus* sp. have longer upper limbs and forearms relative to their lower limbs (Aiello and Wood, 2002). This pattern shifts at about 1.8–1.6 mya with the emergence of *H. erectus*/*H. ergaster* (KNM-WT 15000) who have longer lower relative to upper limbs and markedly reduced forearms (Holliday, 2012; Jungers, 2009). *Australopithecus*-like body size and proportions of Late Pleistocene hominin Liang Bua fossils are unique for their temporal and spatial location. The humerus (243 mm) and femur (280 mm) of Liang Bua (LB) 1 produce an extremely high humerofemoral index at 0.868 (Jungers et al., 2009b; Larson et al., 2009), just above that of *Australopithecus afarensis* (A.L. 288-1 at 0.845–0.854; Holliday, 2012; Jungers, 2009). LB1 also displays an *Australopithecus*-like, high intermembral index with a range of 0.87–0.88. The intermembral index was calculated as a range using the estimated lengths of ulna LB1/52 (205 mm) and radius LB3 (210 mm), with length data for the humerus (243 mm), femur (280 mm) and tibia (235 mm) of LB1 taken from Jungers et al. (2009b) and Larson et al. (2009).

To better understand these proportions, research has focused on scaling relationships between body size and morphological traits of small- to large-bodied hominins (Jungers, 2009; Holliday and Franciscus, 2009, 2012). Femoral length of LB1 roughly follows

allometric regressions for a hominin scaled down to a smaller body mass; in hominins, femoral length scales isometrically or with slight positive allometry. However, with a significantly shorter femur for its body mass (-18.1% to -21.5% (Holliday and Franciscus, 2009), LB1 is on the extreme of this trend and aligns more closely with the regression patterns seen in *Pan*. Similar research identified that A.L. 288-1 and LB1 have humeri longer than expected for their predicted body masses (Holliday and Franciscus, 2012). These comparisons assume that LB1 follows static allometric trends similar to modern humans and mainland hominins. Little is known about the allometric trajectory for this individual, due to a dearth of information about population variation of LB1.

Importantly, research has found that allometric relationships between body size and morphological traits follow unique trends for an island dwarf, even when compared to their closely related, non-dwarfed, ancestor (Gould, 1971; Marshall and Corruccini, 1978; Roth, 1992; Shae and Gomez, 1988; Sondaar, 1977; Weston and Lister, 2009). Further, island dwarfs tend to follow different patterns of limb scaling compared to non-dwarfs for a given species (Sondaar, 1977). These scaling relationships indicate that conclusions about the unique morphology of LB1 would benefit from analyses on population variation of island dwarfs compared to their mainland counterparts. The goal of this research is to better understand the scaling of limb proportions to body size for a population of dwarfed island organisms. In doing so, this research proposes a novel way of explaining the unique limb size and proportions of the diminutive Late Pleistocene hominin fossil, LB1.

Recognizing that island dwarfs may have unique morphology, Weston and Lister (2009) provided insights on brain and body size allometry of LB1. By looking at a

dwarfed island hippo they inferred that the cranial capacity of LB1 is not abnormal for a *H. erectus* population who adapted to an island environment by dwarfing. This research supports *H. floresiensis* as a distinct hominin species, and not a pathological variant (Lieberman, 2009). However, originally noted by Foster (1964) and later confirmed by subsequent researchers, island dwarfing is a convergent adaptation that varies based on the original size of the organism, community ecology (such as predator-prey dynamics), and degree of isolation (Case, 1978; Lomolino, 2005; Lomolino et al., 2012). Hominins and hippos vastly differ in these parameters. Differential pressures would be placed on their island populations due to differences in their ecological niches, which may result in divergent dwarfed phenotypes (van der Geer, 2014). It is becoming increasingly apparent that the ecological niche of the ancestral species and subsequent community structure of the inhabited island are significant context in determining patterns of island dwarfing (Lomolino et al., 2012; Raia and Meiri, 2006). A better comparative model that accounts for the ecological context of LB1 is necessary.

When an organism migrates to an island, its ecological niche has specific constraints that affect if and how its body size may become reduced. Herbivores are limited by the amount and type of primary productivity within an area (Crawley, 1983), their ability to extract nutrients from these resources (Illius and Gordon, 1992), and their capacity to interspecifically compete for resources and defend themselves (Morse, 1980; Stanley, 1979). In island ecosystems with finite resources and a lack of interspecific competition, large body size is no longer advantageous. Further, as body size is negatively correlated with population density, higher population density of smaller individuals decreases extinction risk (Brown and Maurer, 1986; Damuth, 1993; Gaston and Lawton, 1988). The

phenotypes of large herbivores on islands are shaped by intraspecific competition to efficiently extract available resources. On islands with finite resources that lack predators, large endothermic herbivores such as *Mammuthus columbi* dwarfed to a size about five times smaller to the form *M. exilis* (Larramendi, 2016). Additionally, dwarfed island herbivores have altered limbs that may improve locomotive abilities around island resources (Sondaar, 1977; van der Geer, 2014). Some limb alterations include: fused and reduced distal elements for low-gear locomotion (common in island ruminants, e.g., *Candiacervus*, *Hoplitomeryx*, and *Phanourios*; Leinders and Sondaar, 1974; van der Geer, 2005), and columnar orientation of the limbs corresponding with a lesser degree of torsion of proximal elements (*Elphas falconeri*; Ambrosetti, 1968). Other modifications may be a product of allometric scaling, including relatively large molars and/or hypsodonty (*Hippopotamus minor*), missing premolars (*Phanourios minor*; Sondaar, 1977), and decreased pneumatization of the skull (*E. falconeri*; Sondaar and Boekschoten, 1967).

Carnivores are dependent upon the presence of primary or secondary consumers within the environment and require necessary phenotypic adaptations to catch them (Gittelman, 1985; Rosenzweig, 1966). Strict carnivores are relatively rare on islands. This may be due to their inability to physically migrate to and colonize oceanic islands without the presence of adequate prey. However, wolves (*Canis lupus hodophilax*), tigers (*Panthera tigris sondaica*), and leopards (*Neofelis diardi*) all evolved on islands and have slightly altered phenotypes compared to mainland forms (Christiansen, 2008; Ishiguro, 2010; Mazák, 1981). Observed differences between carnivores on islands and their mainland ancestors have been reported for craniodental characteristics and coat coloring

(Christiansen, 2008; Mazák and Groves, 2006; Kitchener et al., 2006). *Neofelis diardi* exhibit markedly divergent craniodental characteristics compared to mainland *N. nebulosa* that approach the primitive tooth form of saber-toothed felids (Christiansen, 2008). Large-bodied endothermic carnivores generally do not exhibit dwarfed body size like large-bodied endothermic herbivores (Burness et al., 2001). Lyras and van der Geer (2006), however, found that a small-bodied Pleistocene island canid (*Cynotherium sardous*) displayed reduced limbs potentially as a response to catching smaller-bodied prey.

While omnivores are consumers, they are not dependent upon the presence of primary or secondary consumers like strict carnivores are. Omnivores can supplement their diet with available primary producers in times of scarcity to maximize nutrient intake (Coogan et al., 2014). Though, research has indicated that feeding preferences of omnivores may be influenced by their herbivorous or carnivorous ancestry (Cooper, 2002; Eubanks, 2005). The fitness of omnivores is often strongly affected by diet mixing and predator avoidance (Sih and McCarthy, 2002; Singer and Bernays, 2003). In an island ecosystem with a dearth of predators, predator avoidance would not be significant, but diet mixing would still be necessary. Deriving from the Order Carnivora, but classified behaviorally and anatomically as omnivores, island raccoons (*Procyon pygmaeus*), coatis (*Nasua nelson*), and foxes (*Urocyon littoralis*) eat a combination of fruit, vegetation, insects, lizards, mice, and crabs (Cuarón et al., 2009; McFadden et al., 2006; Roemer et al., 2001). Cozumel dwarfed raccoons differ from *P. lotor* in morphological traits, including: broad black throat band, golden yellow tail, short posteriorly and rounded nasals, reduced teeth, and a 20% reduction in body size (Cuarón,

et al. 2009; Merriam 1901). Dwarfed coatis on Cozumel significantly reduced their body size to 30–38% of *N. narica* and have a reduced cranium as well (Cuarón et al., 2009). Dwarfed foxes on the Channel Islands, California, archipelago are differentiated from mainland gray foxes (*U. cinereoargenteus*) by cranial shape and a 30% reduction in body size (Collins, 1993; Wayne et al., 2001). While less numerous than herbivores on islands, omnivores (even Carnivora) may convergently share herbivorous body size reduction and skeletal modification trends on islands.

To elucidate the endemic skeletal pattern expected for the dwarfed hominin species, *H. floresiensis*, analyses should be done on body size and shape changes of an island dwarf within a similar ecological niche. Dental and archaeological data suggest that these Late Pleistocene hominins most likely interacted within their ecosystem as omnivores. The wear pattern of the LB1 dentition is most similar to Plio-Pleistocene hominin fossils and modern hunter-gatherers, indicating a significant contribution of plant fiber to their diet (Jungers and Kaifu, 2011; Kaifu, et al. 2015). Faunal deposits associated with diminutive hominin fossils from the Late Pleistocene cave site, Liang Bua, also indicate dietary contribution of juvenile pygmy stegodonts (*Stegodon florensis insularis*), Komodo dragons (*Varanus komodoensis*), endemic giant rats, and birds (Amesbury, 2011; Brumm et al., 2006; Szabó and; Puspaningrum et al., 2014; van den Bergh, et al. 2009). I argue that the best comparative model for interpreting the endemic body size and shape of LB1 is a non-human dwarfed island omnivore.

This study uses samples of dwarfed island foxes (*Urocyon littoralis santacruzae*) and ancestral mainland foxes (*Urocyon cinereoargenteus*) to assess the morphological consequences of dwarfing on limb segments. In doing so, I measured limbs to determine

if dwarfing could be detected through limb segments, if limb elements were proportionally the same, and if static allometries of limb lengths regressed on body size differed for these two samples. While the marked probable differences in body size between foxes and early hominins complicate comparisons, foxes as omnivores are still an excellent model for understanding body size alterations in an island ecology.

## Materials and methods

### *Samples*

Limb proportions and body size of adult island fox (*Urocyon littoralis santacruzae*;  $n = 27$ ) are compared to its mainland adult relative (*U. cinereoargenteus*;  $n = 30$ ). Limbs with fully fused epiphyses were classified as adults and therefore used in this study. The mainland gray fox is from sites located in Santa Barbara County, along the Pacific coast on the mainland of California, located at 34°N latitude. It has a climate classified as mild warm-summer Mediterranean, with temperatures remaining between about 4.4–32.2°C (40–90°F). As predators are present within mainland California, gray foxes alter their foraging behavior and habitat preferences to avoid predation by coyotes and bobcats. They reduce activity during the day and increase activity at night. Additionally, gray foxes may prefer bushy instead of open habitats to avoid predation (Farías et al., 2012).

Also at 34°N latitude, Santa Cruz Island, California belongs to the northern Channel Islands archipelago. Gray foxes reached the northern Channel Islands most likely by human-assisted dispersal from mainland California across a 44.6 km channel roughly 9200–7100 years ago (Collins, 1991; Hofman et al., 2015; Rick et al., 2009).

Santa Cruz Island has a maritime temperate climate with an average high and low at 9.4–21.1°C and (49–70°F). Within 2000 years of arrival to Santa Cruz Island, the gray foxes rapidly underwent a series of body size shifts that eventually produced its current dwarfed form and taxonomic designation as the island fox (*U. littoralis santacruzae*; Hofman et al., 2015). There is no evidence of human consumption of the island fox (Collins, 1991).

Island foxes differ from mainland counterparts by roughly 30% reduction of body size (Collins, 1982; Wayne et al., 2001). Lacking the predation pressures that are present in mainland California, the island fox is more active during the day (Moore and Collins, 1995) and have significantly higher population densities but smaller dispersal rates (Roehmer et al., 2001). While golden eagles have been a predation problem for the island foxes in recent years (Hudgens and Garcelon, 2010), prehistorically, bald eagles were the predominant potential predators of foxes and subsisted primarily on seabird populations (Roemer et al., 2001). The island fox is an omnivore within its island ecosystem, subsisting on seeds, fruits, insects, crabs, birds, deer mice, lizards, and eggs (Collins, 1993; Moore and Collins, 1995). Analysis of fox and human bone isotopes indicate that the foxes were not using anthropogenic resources, rather, they varied their diet following shifts in resource availability and are characterized as generalist foragers (Hofman et al., 2016).

Both the mainland and island fox have a 1:1 sex ratio and are highly monogamous. Sexual dimorphism is present, though, in both species where males are slightly larger in body mass and head-to-tail length than females (Fritzell & Haroldson, 1982; Moore and Collins, 1995; Collins, 1993). Research on cranial and pelvic size

dimorphism of *U. cinereoargenteus* and *U. littoralis* spp. found that the os coxae differed significantly in size and shape between males and females, and these differences were more dramatic in the island fox (Schutz et al., 2009). This suggests that sexual dimorphism in shape associated with changes in size is more prominent in elements associated with parturition. Sexing of the remains was done during initial collection while the skeletons were fleshed and fully articulated. As a result, the mainland sample consists of  $n = 10$  females,  $n = 15$  males, and  $n = 5$  indeterminate. For the island sample, sex was documented for only seven skeletons, yielding a sample of  $n = 3$  females,  $n = 4$  males, and  $n = 20$  indeterminate. Because of the mating behaviors and 0.5 sex ratio of *Urocyon* sp., the probability of unbalanced samples is low, but possible given the small sample sizes (Kościński & Pietraszewski, 2004). Both samples were visually and statistically explored to the extent possible given the small sample sizes during data analysis to identify levels of sexual dimorphism present between the species, and verify that the samples are balanced.

The island fox sample was housed at the Phoebe Hearst Museum of Anthropology, University of California, Berkeley, and the Santa Barbara Museum of Natural History (SBMNH). The mainland gray fox sample was from the SBMNH. The remains represent relatively recent (<500 years before present) skeletons from all over Santa Cruz Island and mainland Santa Barbara, California. The specimens were mostly from articulated individuals who died of natural causes. Limbs from the same individual were analyzed together. Three of the individuals from Santa Cruz Island had a limb bone with a damaged epiphysis from poor preservation, requiring estimation of the full length

of the bone. Estimation was done via multivariate nonparametric missing value imputation with missForest package in R Version 3.6.3 (R Core Team, 2020).

#### *Data analysis*

Maximum lengths of the humerus, radius, femur, and tibia were measured to the nearest 0.01 mm using a digital caliper (Figure 1). Body mass data were made available by the original collectors of the fleshed *Urocyon* sp. skeletons for  $n = 18$  foxes ( $n = 6$  *U. littoralis santacruzae*;  $n = 12$  *U. cinereoargenteus*). Because not all of the skeletons had associated masses ( $n = 39$ ), minimum humeral and femoral diaphyseal circumferences were measured with measuring tape to the nearest 0.01 mm and used to estimate body mass; these circumferences are reported to be tightly correlated with body mass across adult mammalian and reptilian quadrupeds of diverse locomotor postures and gaits (Anderson et al., 1985; Christiansen, 1999; Campione and Evans, 2012).

To identify the best equation to use for body mass estimation of *Urocyon* sp., Percent Prediction Error (PPE; Smith, 1980) was calculated for four published equations (Table 1). Published body mass equations aim to identify universal scaling laws that are useful across diverse taxa. However, the explanatory power of interspecies equations for body mass of a single species may be significantly reduced. To circumvent this potential problem, each published equation was tested against *Urocyon* sp. skeletons with known body mass information. These data are associated with the osteological parameters used to estimate body mass following equations in Anderson et al. (1985), Christiansen (1999), and Campione and Evans (2012). To select the most appropriate body mass estimation method for *Urocyon* sp. skeletons with unknown body mass, PPE was calculated for each equation as:

$$PPE = \left( \frac{\text{Measured} - \text{Predicted}}{\text{Predicted}} \times 100 \right),$$

following Smith (1980). Table 1 summarizes the equations extracted from the literature, along with their reported R<sup>2</sup> values and calculated PPE. The equation taken from Campione and Evans (2012) had the lowest PPE (12.78%) and was therefore selected to estimate the fox body masses for analyses. Body mass estimates were calculated using the MASSTIMATE package in R with the MR function (Campione and Evans, 2012) to calculate phylogenetically-corrected body mass estimations (Table 1).

To assess whether the  $n = 20$  indeterminate island fox skeletons were sex-balanced, level of sexual dimorphism of the known, sex-balanced, mainland fox sample ( $n = 25$ ) were identified using the coefficient of variation of predicted body mass (Plavcan, 1994; Kościński and Pietraszewski, 2004). The predicted body mass CV for the mainland fox then was compared to the predicted body mass CV for the island fox. If the island fox sample has a significantly different level of sexual dimorphism, and therefore an unbalanced sex-sample, its predicted body mass CV should be significantly different from the mainland fox ( $p < 0.05$ ). Differences in the predicted body mass CV between samples was tested using the asymptotic test for the equality of coefficients of variation from k populations (Feltz and Miller, 1996) in the cvequality package in R. Predicted body mass CVs did not differ significantly between the two samples (mainland CV = 14.07, island CV = 12.98;  $p = 0.68$ ). This suggests that levels of sexual dimorphism in body mass are not significantly different between the two samples; the island fox sample is likely sex-balanced, similar to the mainland fox sample.

To test for differences in size and limb proportions between island and mainland foxes, Welch's two sample *t*-tests were used to compare humerus, radius, femur, and tibia

lengths, and limb indices in the two samples. Differences in limb proportions were assessed between the two samples for the brachial, crural, intermembral, and humerofemoral indices. Size of elements and limb proportions between island and mainland foxes were deemed significantly different if the *p*-value was less than 0.05. Following Allen's Rule (1877), I predicted that these closely related and climatically similar species will not differ significantly in limb proportions.

To explore body size and limb allometry within and between samples, all measurements were  $\log_{10}$  transformed for linearity and assessed using Ordinary Least Squares (OLS) regression. OLS regressions are used because the purpose of this study is to predict the effect that body mass (X) has on limb element size (Y) of the two samples (Smith, 2009). Reduced Major Axis (RMA) regressions tends to overestimate slopes and have low statistical power when sample sizes are small and parametric correlation is less than 0.60 (Smith, 2009; Jolicoeur, 1975).

Body mass was chosen as the size measure because it is involved in ecological, biological, and structural negotiations of an adult organism, which are of particular interest when exploring body size dwarfing on islands. First, body mass scales with basal metabolic rate (BMR) on average among species to the power of  $\frac{3}{4}$  (Kleiber, 1935; Darveau et al., 2002; West et al., 1997). Consequently, the mass of an organism has effects on its nutritional demands. This can constrain consumer-resource relationships, such that body mass is inversely correlated with trophic level status (Brose, 2010; Arim et al., 2010; Petchey, et al. 2008). For example, larger organisms with greater body masses generally have lower BMRs, greater resource predictability, and a lower cost of

transportation. This suite is favored in large herbivores who spend most of their day grazing or browsing and avoiding predation.

Second, body mass places stresses upon the long bones of organisms, necessitating alterations to the length and diameter of limb elements to prevent failure. Geometric and elastic models predict the rates at which long bone length and diameter should scale to body mass (Garcia et al., 2006; Christiansen, 1999; Campione and Evans, 2012). Empirical results found that despite the great diversity in length and shape of long bones across organisms, peak stresses on these systems tend to be similar regardless of size (Rubin and Lanyon, 1984). This is produced by adjustments to the length and shape of long bones, and posture of limbs (Garcia et al., 2006). Species within the Order Carnivora tend to show geometric scaling of limb length to body mass but elastic scaling of limb circumference to body mass (Christiansen, 1999; Campione and Evans, 2012). Thus, the resulting body mass and long bone shape of an organism is the product of a balance among consumer-resource dynamics and structural requirements of the limbs.

As an organism evolves in an island environment, changes in body mass should follow changes in consumer-resource dynamics. Limb size, shape, and posture should also be adjusted to fulfill the structural demands of the organism. Limb length and postural changes associated with body mass are tightly constrained for species within Carnivora, where regression analyses indicate similar allometric trends among species (Wayne, 1986; Bertram and Biewener, 1990). Therefore, I predicted changes in body mass of the island fox to correspond with alterations of the limbs that closely follow trends seen in the mainland fox sample.

Limb lengths were regressed on predicted body mass using OLS to identify the slopes and intercepts for each species and their R<sup>2</sup> and standard error (SE) values. If the relative contributions of elements to total size are equivalent between the island and mainland fox, their slopes and intercepts should be similar. To test for similar slopes and intercepts, pairwise comparisons using analysis of covariance (ANCOVA) and two sample *t*-tests, respectively, were done for each log<sub>10</sub> limb against log<sub>10</sub> predicted body mass. Assumptions for normality for each variable and homoscedasticity for each Y value of X were tested prior to analysis. Normality and homoscedasticity were visually and statistically inspected using the Shapiro-Wilk test for normality and Breusch-Pagan test for homoscedasticity. All variables for both samples were found to be normally distributed and homoscedastic. ANCOVA was run to test for similar slopes by testing for the interaction between body mass and limb lengths with species as the factor. If slopes did not significantly differ ( $p > 0.05$ ), intercepts were tested for similarity with a two-sample *t*-test where  $t = \left( \frac{b_1 - b_2}{SE_{b_1}} \right)$  and b<sub>1</sub> and b<sub>2</sub> are the intercepts for each group and SE is the standard error of the OLS regression (Zar, 1968). All statistical analyses were run in R.

## Results

Island foxes have a 48% reduction in body mass compared to the mainland gray fox. This dramatic body mass decrease is accompanied by significant reductions in limb lengths. Island foxes have significantly shorter limbs than mainland foxes ( $p < 0.05$ ; Table 2). On average, the island fox limbs are about 24% shorter than those of the mainland fox. Changes in limb length also indicate changes in limb proportions between

the two species. The island fox has a significantly greater brachial index (87.62;  $p = 0.02$ ), and significantly smaller intermembral (81.87;  $p = 0.01$ ) and humero femoral (89.93;  $p < 0.01$ ) index compared to the mainland fox (brachial, intermembral, and humero femoral indices of 86.63, 82.73, and 91.22, respectively). The crural index does not differ significantly ( $p = 0.51$ ) between the two groups.

OLS regression results are provided in Tables 3 and 4, and can be visualized in Figures 4 and 5. When limb element length is regressed on predicted body mass, all slopes are significantly different between the two populations ( $p < 0.05$ ). The island fox has significantly steeper slopes for all limb lengths regressed on predicted body mass (Table 3). Because all slopes differ significantly, tests for intercept similarities were not performed. The island fox has smaller intercepts indicating their limbs are absolutely smaller but decrease in length at a greater rate relative to body mass compared to the mainland fox. If the mainland fox were scaled down to the size of an island fox, following mainland, gray fox within-population allometric trajectories, the mainland fox would have limbs absolutely longer for its body mass. The island fox limb to body mass allometric trends significantly diverge from what is predicted for a mainland fox. The island fox is not merely a scaled down version of the mainland fox.

## Discussion

### *Body size and limb scaling of the island fox*

This study provides valuable data that supplement our understanding of scaling trends between closely-related island and mainland species. Foxes of the genus *Urocyon* that interact with their ecological system as omnivores, show significant size reductions

after evolving in an island environment with relatively few predators and limited resources. Body mass is significantly reduced in *U. littoralis santacruzae* (island fox) corresponding with changes in population dynamics. Increased population density and intraspecific competition, and reduced dispersal are consistent with significant reductions of body mass in the island fox. Further, these changes in body mass correspond with changes in the lengths and proportions of limbs that do not follow the allometric trends of *U. cinereoargenteus* (mainland fox).

Assessing the static allometry of traits against body mass of island populations compared to ancestral mainland counterparts can illuminate how unique traits evolve in conjunction with body size in dwarfed species. Numerous studies have demonstrated that static allometric coefficients (including the slope and intercept) of a trait regressed on body mass can vary among populations who are under different selective pressures (Anzai et al., 2017; Bourndasky 2007; Ergest et al., 2011, 2012; Newell, 1949; Pélabon et al., 2013; White and Gould, 1965). Intercept differences between two regressions of a given trait on body mass can result from changes in selective pressures on the mean size of that trait, while the slope tends to remain static among species and populations (Ergest et al., 2011, 2012). This indicates that changes in community-resource dynamics, resulting in differential selective pressures, likely contributed to the differences in the mean size of limb length between the island and mainland foxes. Changes in the static allometric slope are less common between two closely-related groups, and may be indicative of changes in growth as ontogenetic and static allometries are correlated (Pélabon et al., 2013). Future research should explore ontogenetic allometric trajectories

of limb lengths regressed on body masses of an island population compared to those of mainland counterparts to assess changes in growth.

Importantly, these results suggest that limb proportions in the diminutive island fox may also reflect changes in selective pressures in a novel island ecosystem. The ability of the island fox to forage for increased vegetation in a prey-reduced environment, and hunt and capture small prey would be improved by limb proportions that support these behaviors. Limb proportions indicate that while the forelimb is proportionally smaller compared to the hindlimb (intermembral = 89.93 vs. 91.22), the forelimb distal element, the radius, is proportionally longer than its proximal element, the humerus, (brachial = 87.62 vs. 86.63) for the island fox. Longer hindlimbs and distal elements improve jumping and small-prey capture performance (Meachen-Samuels and Van Valkenburgh, 2009; Harris and Steudel, 1997), which would be particularly useful in the capture of island prey such as crabs, mice, and lizards. Body mass alterations following changes to ecosystem dynamics in island niches have corresponding limb adjustments that may reflect altered consumer-resource behavior for omnivores. Conversely, selective pressures for smaller body mass in the island fox may have inadvertently produced limb proportions that are unique merely as an unselected byproduct of dramatic body size reduction (Gould and Lewontin, 1979). Further, founder effects and genetic drift commonly occur in insular ecologies, and may also have contributed to divergent body proportions in this island sample (Mayr, 1942). More research should examine population variation of a dwarfed island species compared to a mainland relative within the context of its ecological niche to understand patterns of trait divergence. Studying how traits of diverse island dwarfs change with body size in response to novel ecosystem dynamics

may elucidate the evolutionary underpinnings of insular dwarfism, including its functional and biological advantages.

### *Implications for Homo floresiensis*

Caution should be exercised when comparing island species to their mainland counterparts. Single fossils plotted along regressions lines from island individuals may significantly diverge from the trend of closely-related mainland species. Differences in relative size of a trait may not represent a phylogenetic signal, but rather an adaptive response to a novel island environment. The omnivorous foxes used in this study show a dramatic body mass reduction that corresponds with distinct limb lengths and proportions in an isolated ecological system with altered community members and resources.

On the island of Flores, Indonesia, in the Late Pleistocene, the omnivore *H. floresiensis* may have displayed *Australopithecus*-like size and proportions not due to immediate ancestry but from adaptations to the island environment. *Homo floresiensis* had significantly shorter upper and lower limbs than any other hominin during the Middle to Late Pleistocene. Further, their limb proportions are characterized as having significantly high intermembral and humerofemoral indices. While these body proportions were last seen with hominins in East Africa in the Early Pleistocene (Aiello and Wood, 2002), there is currently no evidence of *Australopithecus* sp. or *H. habilis* outside of Africa. Recent discoveries at a Middle Pleistocene site (Mata Menge) on Flores point to diminutive size being achieved by at least ~0.7 mya (van den Bergh et al., 2016). The only hominin fossils that precede the Liang Bua and Mata Menge fossil assemblage near Flores in Indonesia belong to *H. erectus*. West of Wallace's Line

(Wallace, 1859), and therefore periodically connected to Sundaland during the Pleistocene, Java has fossil material attributed to *H. erectus*, including: Trinil 1 and 2 (0.7–1 mya; Theunissen, 1989), Sangiran 2 (1.25 mya; Larick et al., 2001), Ngandong (143–546 kya; Rizal et al., 2020), and Mojokerto (1.8 mya?; Morwood et al., 2003). Therefore, it seems likely that *H. erectus* migrated East of Wallace's Line to Flores and became isolated with unique selective pressures.

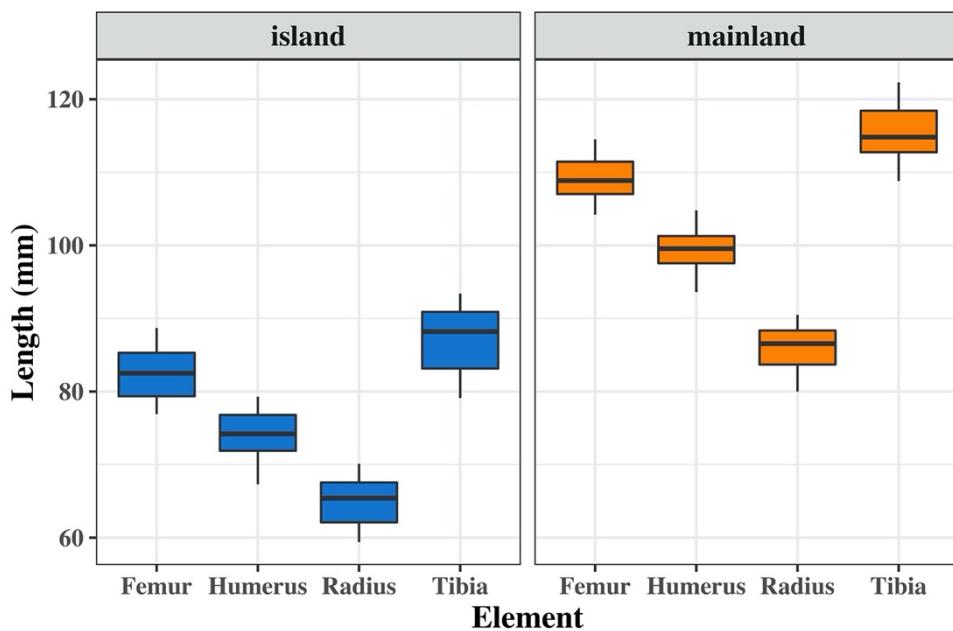
Divergences from ancestral *H. erectus* body mass and limb length scaling in *H. floresiensis* is plausible and should arguably be expected. Research has suggested that at about 1.8–1.6 mya the genus *Homo* developed longer lower limbs not only as a thermoregulatory response, but also due to greater locomotive efficiency as they expanded their ranges (Polk, 2004; Pontzer, 2007; Holliday, 2012). If this omnivorous biped became isolated on an island with finite resources and few predators, lower limbs for increased locomotor efficiency and diet breadth expansion may not have had a fitness advantage anymore. Rather, selection for smaller body mass via reductions in stature would be favored in an isolated environment that potentially has increased intraspecific competition for limited resources. Alterations in body mass would have differential scaling effects on limbs within this novel island environment, potentially producing limbs that diverge from what is expected for their body mass (Holliday and Franciscus, 2012). Additionally, adjustments to the limbs corresponding with changes in body mass in an island ecosystem may be responsible for the significantly different limb proportions of LB1. These changes may be reflective of altered predator and resource-extraction behavior in the novel island community of Flores.

## **Acknowledgements**

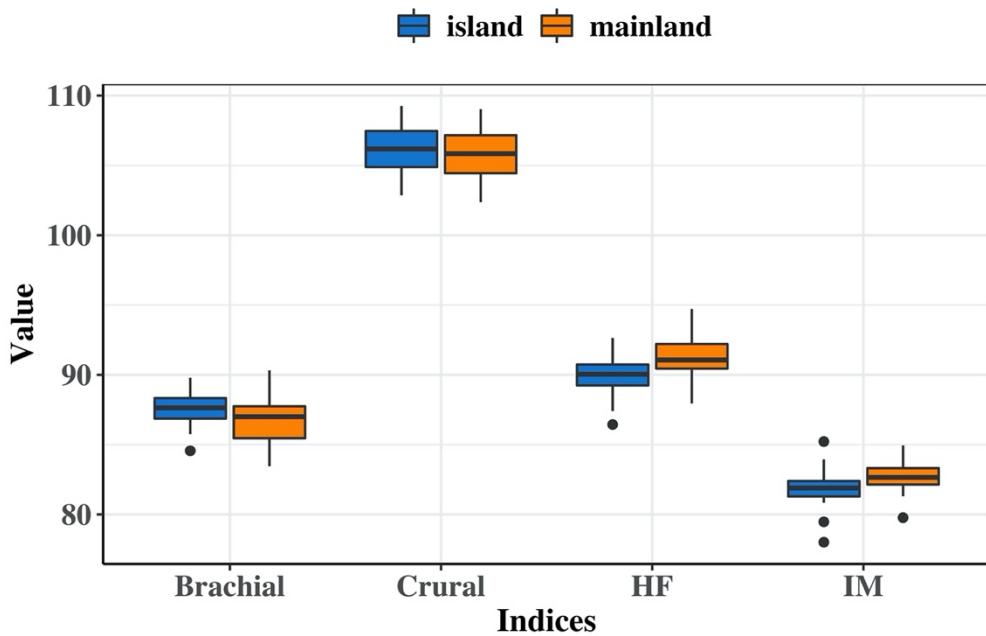
This work was supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1443129. Special thanks to the following individuals and institutions for access to these important collections: Natasha Johnson (Phoebe Hearst Museum of Anthropology, UC Berkeley) and Paul Collins (Santa Barbara Museum of Natural History). This paper greatly improved through the detailed and thoughtful comments of three anonymous reviewers and from conversations and edits from Libby Cowgill, Karthik Panchanathan, Matthew Gompper, Lana Kerker Oliver, Agustin Fuentes, and Scott Maddux. Lastly, theoretical ideas for this paper were refined while working with John Nahon at the St. Louis Science Center and teaching basic ecological concepts to diverse museum audiences.



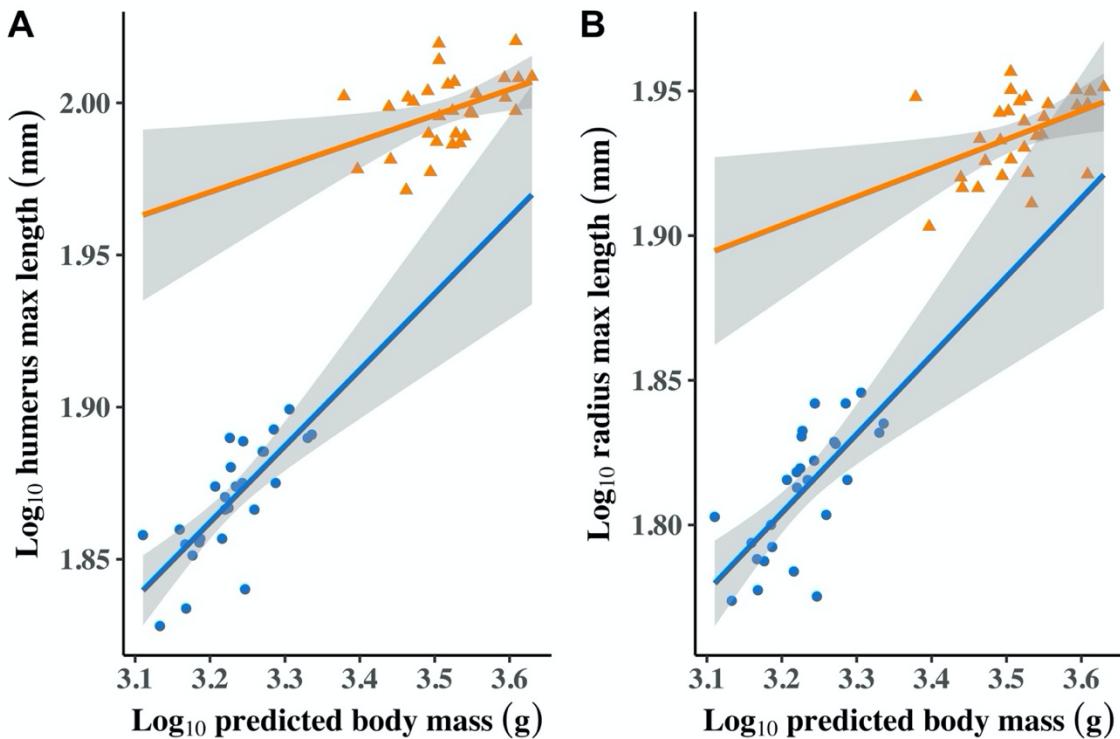
**Figure 3.1: Elements of foxes (*Urocyon* sp.) used in analysis. From left to right: femur, tibia, radius, and humerus of *U. littoralis santacruzae*. Dotted lines indicate maximum length measures taken on each element to the nearest 0.01mm. FML = femur max length; TML= tibia max length; RML = radius max length; HML = humerus max length.**



**Figure 3.2: Box plots of mainland (*Urocyon cinereoargenteus*) and island (*U. littoralis santacruzae*) fox limb element lengths (mm).**

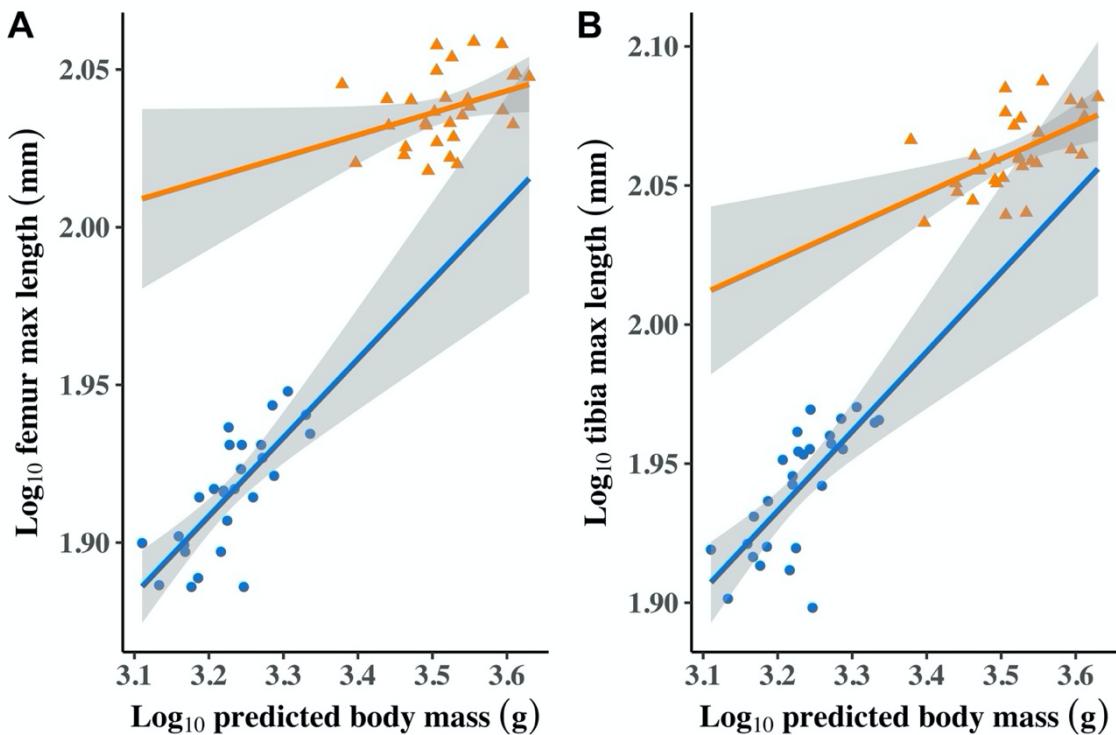


**Figure 3.3: Box plots of mainland (*Urocyon cinereoargenteus*) and island (*U. littoralis santacruzae*) limb indices. The island fox has a significantly higher brachial index ( $p = 0.02$ ), and significantly lower humero femoral (HF) index ( $p = 0.01$ ), and intermembral (IM) index ( $p < 0.01$ ).**



**Figure 3.4: Scatter plot of log<sub>10</sub> proximal and distal forelimb elements (mm)**

regressed on log<sub>10</sub> predicted body mass (g) for island (*Urocyon littoralis santacruzae*) and mainland (*U. cinereargenteus*) foxes. Island foxes are indicated by blue circles, mainland foxes are indicated by orange triangles. LS line is fitted through each sample along with their 95% confidence limits in grey shade. Plot A: island fox OLS formula:  $Y = 0.25X + 1.06$ ; mainland fox OLS formula:  $Y = 0.08X + 1.70$ . Plot B: island fox OLS formula:  $Y = 0.27X + 0.93$ ; mainland fox OLS formula:  $Y = 0.10X + 1.59$ .



**Figure 3.5: Scatter plot of log<sub>10</sub> proximal and distal hindlimb elements (mm) regressed on log<sub>10</sub> predicted body mass (g) for island (*Urocyon littoralis santacruzae*) and mainland (*U. cinereargenteus*) foxes. Island foxes are indicated by blue circles, mainland foxes are indicated by orange triangles. LS line is fitted through each sample along with their 95% confidence limits in grey shade. Plot A: island fox OLS formula: Y = 0.25X + 1.11; mainland fox OLS formula: Y = 0.07X + 1.79. Plot B: island fox OLS formula: Y = 0.29X + 1.02; mainland fox OLS formula: Y = 0.12X + 1.63.**

**Table 3.1: Body mass estimation equations and calculated PPE.**

<b>Y = aX<sup>b</sup></b>	<b>a</b>	<b>b</b>	<b>Reported R<sup>2</sup></b>	<b>Calculated PPE<sup>a</sup></b>
<b>Christiansen, 1999<sup>b</sup> (Carnivora; Y = humeral circumference)</b>	13.924	0.3893	0.988	20.75%
<b>Christiansen, 1999<sup>b</sup> (Carnivora; Y = femoral circumference)</b>	14.928	0.3592	0.988	17.27%
<b>Anderson et al., 1985<sup>c</sup> (Terrestrial quadruped; X = humeral + femoral circumference)</b>	0.078	2.73	0.92	15.75%
<b>Campione &amp; Evans, 2012<sup>d</sup> (Equation 6 using phylogenetic correction; Y = humeral + femoral circumference)</b>	0.079	2.745	0.988	12.78%

<sup>a</sup>Each equation estimated the body mass of foxes with known weights (n=18). After, a Percent Prediction Error (PPE) was calculated for each equation against the known body mass as (Measured-Predicted)/Predicted x 100. All estimates were converted to grams before calculating PPE.

<sup>b</sup>Christiansen, 1999 use natural log, osteological parameters (in mm) as Y, body mass (in kg) as X.

<sup>c</sup>Anderson et al., 1985 use log<sub>10</sub>, osteological parameters (in mm) as X, and body mass (in g) as Y.

<sup>d</sup>Campione & Evans, 2012 use log<sub>10</sub>, osteological parameters (in mm) as X, and body mass (in g) as Y.

**Table 3.2: Descriptive statistics and results from Welch's two-sample *t*-test for island (*Urocyon littoralis santacruzae*) and mainland (*U. cinereoargenteus*) fox samples.**

	<b><i>Island fox (n=27)</i></b>	<b><i>Mainland fox (n=30)</i></b>	<b><i>Two-sample t-test</i></b>			
	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b><i>t</i>-score</b>	<b><i>P</i>-value</b>
HML <sup>a</sup>	74.04	3.14	99.46	2.75	-32.35	<0.001
RML <sup>b</sup>	64.89	3.24	86.16	2.75	-26.57	<0.001
FML <sup>c</sup>	82.34	3.51	109.05	2.97	-30.81	<0.001
TML <sup>d</sup>	87.37	4.43	115.34	3.67	-25.74	<0.001
Body mass (g)	1702.50	220.97	3329.67	468.40	-17.04	<0.001
Brachial index	87.62	1.30	86.63	1.75	2.45	0.02
Crural index	106.09	1.81	105.77	1.79	0.07	0.51
Intermembral index	81.87	1.35	82.73	1.06	-2.63	0.01
Humerofemoral index	89.93	1.37	91.22	1.61	-3.27	0.002

<sup>a</sup>Humerus maximum length in millimeters.

<sup>b</sup>Radius maximum length in millimeters.

<sup>c</sup>Femur maximum length in millimeters.

<sup>d</sup>Tibia maximum length in millimeters.

**Table 3.3: Slope, intercept, standard error (SE), and R<sup>2</sup> of OLS line-fitting technique for log<sub>10</sub> limb lengths (mm) regressed on log<sub>10</sub> predicted body mass (g) for island (*Urocyon littoralis santacruzae*) and mainland (*U. cinereoargenteus*) fox samples.**

~ Body mass (g)		Slope	SE <sub>slope</sub>	Intercept	SE <sub>intercept</sub>	R <sup>2</sup>	P-value
<b>HML<sup>a</sup></b>	Island	0.25	0.04	1.06	0.14	0.58	<0.001
	Mainland	0.08	0.03	1.70	0.12	0.19	0.02
<b>RML<sup>b</sup></b>	Island	0.27	0.06	0.93	0.18	0.49	<0.001
	Mainland	0.01	0.04	1.59	0.14	0.19	0.02
<b>FML<sup>c</sup></b>	Island	0.25	0.04	1.11	0.14	0.57	<0.001
	Mainland	0.07	0.03	1.79	0.12	0.13	0.05
<b>TML<sup>d</sup></b>	Island	0.29	0.06	1.02	0.18	0.52	<0.001
	Mainland	0.12	0.04	1.63	0.12	0.29	0.002

<sup>a</sup>Humerus maximum length in millimeters.

<sup>b</sup>Radius maximum length in millimeters.

<sup>c</sup>Femur maximum length in millimeters.

<sup>d</sup>Tibia maximum length in millimeters.

**Table 3.4: Statistics and *P*-values from comparing slopes and intercepts for OLS regressions of  $\log_{10}$  limb lengths (mm) regressed on  $\log_{10}$  predicted body mass<sup>0.33</sup> (g) for island (*Urocyon littoralis santacruzae*) and mainland (*U. cinereoargenteus*) fox samples.**

	Slopes are equal		Intercepts are equal	
	ANCOVA		Two-sample <i>t</i> -test	
	<i>F</i> -score	<i>P</i> -value	<i>t</i> -score	<i>P</i> -value
HML:Mass <sup>0.33</sup>	8.55	0.005	-4.57	<0.001
RML:Mass <sup>0.33</sup>	6.12	0.017	-3.67	<0.001
FML:Mass <sup>0.33</sup>	9.91	0.003	-4.86	<0.001
TML:Mass <sup>0.33</sup>	5.89	0.019	-3.39	<0.001

<sup>a</sup>Humerus maximum length against predicted body mass<sup>0.33</sup>.

<sup>b</sup>Radius maximum length against predicated body mass<sup>0.33</sup>.

<sup>c</sup>Femur maximum length against predicted body mass<sup>0.33</sup>.

<sup>d</sup>Tibia maximum length against predicted body mass<sup>0.33</sup>.

## Literature Cited

- Aiello LC. 2010. Five years of *Homo floresiensis*. Am J Phys Anth. 142:167–179.
- Aiello LC, Wood B. 2002. Early hominin limb proportions. J Hum Evo 43:529–548.
- Allen J. 1877. The influence of physical conditions in the genesis of species. Rad Rev 1:108–140.
- Ambrosetti P. 1968. The Pleistocene dwarf elephants of Spinagallo (Siracusa, SouthEastern Sicily). Geo Romana VII 277–397.
- Anderson JF, Hall-Martin A, Russell DA. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. J Zool 207:53–61.
- Anzai H, Oishi K, Kumagai H, Hosoi E, Nakanishi Y, Hirooka H. 2017. Interspecific comparison of allometry between body weight and chest girth in domestic bovids. Sci Rep 7:1–7.
- Argue D, Donlon D, Groves C, Wright R, 2006. *Homo floresiensis*: microcephalic, pygmy, *Australopithecus*, or *Homo*? J Hum Evo 51:360–374.
- Bertram JEA, Biewener AA. 1990. Differential scaling of the long bones in the terrestrial Carnivora and other mammals. J Morpho 204:157–169.
- Bonduriansky R. 2007. Sexual selection and allometry: a critical reappraisal of the evidence and ideas. Evolution 61:838–849.
- Brisbin IL Jr, Lenarz MS. 1984. Morphological comparisons of insular and mainland populations of Southeastern white-tailed deer. J Mammal 65:44–50.
- Bromham L, Cardillo M. 2007. Primates follow the ‘island rule’: implications for interpreting *Homo floresiensis*. Biol Lett 3:398–400.
- Brown JH, Maurer BA. 1986. Body size, ecological dominance, and Cope’s rule. Nature 324:248–250.

- Brown P, Maeda T. 2009. Liang Bua *Homo floresiensis* mandibles and mandibular teeth: a contribution to the comparative morphology of a new hominin species. *J Hum Evo* 57:571–596.
- Brown P, Sutikna T, Morwood MJ, Soejono RP, Sapomo EW, Due RA. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:248–250.
- Brumm A, Aziz F, van den Bergh GD, Morwood MJ, Moore MW, Kurniawan I, Hobbs DR, Fullagar R. 2006. Early stone technology on Flores and its implications for *Homo floresiensis*. *Nature* 441:624–628.
- Burness GP, Diamond J, Flannery T. 2001. Dinosaurs, dragons, and dwarfs the evolution of maximal body size. *PNAS USA* 98:14518–14523.
- Case TJ. 1978. A general explanation for insular body size trend in terrestrial vertebrates. *Ecology* 59:1–18.
- Christiansen P. 1999. Scaling of the limb long bones to body mass in terrestrial mammals. *J Morpho* 239:167–190.
- Christiansen P. 2008. Species distinction and evolutionary differences in the clouded leopard (*Neofelis nebulosa*) and Diard's clouded leopard (*Neofelis diardi*). *J Mammal* 89:1435–1446.
- Collins PW. 1991. Interaction between island foxes (*Urocyon littoralis*) and Indians on islands off the coast of Southern California: I. Morphologic and archaeological evidence of human assisted dispersal. *J Ethnobiol* 11:51–81.
- Collin PW. 1993. Taxonomic and biogeographic relationships of the island fox (*Urocyon littoralis*) and gray fox (*U. cinereoargenteus*) from Western North America. Third California Islands Symposium, 351–390.

- Coogan SC, Raubenheimer D, Stenhouse GB, Nielson SE. 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis. *PLoS One* 9:e97968.
- Cooper Jr W. 2002. Convergent evolution of plant chemical discrimination by omnivorous and herbivorous scleroglossan lizards. *J Zool* 257:53–66.
- Crawley MJ. 1983. *Herbivory: The Dynamics of Animal-Plant Interactions*. Blackwell Scientific Publications, Oxford.
- Cuarón AD, Valenzuela-Galvan D, Garcia-Vasco D, Copa ME, Bautista S, Mena H, Martinez-Godinez D, Gonzalez-Baca C, Bojorquez-Tapia LA, Barraza L, de Grammont PC. 2009. Conservation of the endemic dwarf carnivores of Cozumel Island, Mexico. *Small Carnivore Conservation* 41:15–21.
- Damuth J. 1993. Cope's rule, the island rule, and the scaling of mammalian population density. *Nature* 365:748–750.
- Ergest CK, Bolstad GH, Rosenqvist G, Endler JA, Pélabon C. 2011. Geographical variation in allometry in the guppy (*Poecilia reticulata*). *J Evolution Biol* 24:2631–2638.
- Ergest CK, Hansen TF, Le Rouzic A, Bolstad GH, Rosenqvist G, Pélabon C. 2012. Artificial selection on allometry: change in elevation but not slope. *J Evolution Biol* 25:938–948.
- Eubanks MD. 2005. Predaceous herbivores and herbivorous predators—the biology of omnivores and the ecology of omnivore—prey interactions. In: Barbosa, P., Castellanos, I. (Eds.), *Ecology of predator–prey interactions*. Oxford University Press, New York, 3–17.
- Falk D, Hildebolt C, Smith K, Morwood MJ, Sutikna T, Brown P, Jatmiko, Sapomo WE, Brunsden B, Prior F. 2005. The brain of LB1, *Homo floresiensis*. *Science* 308:242–245.

- Farías V, Fuller TK, Sauvajot RM. 2012. Activity and distribution of gray foxes (*Urocyon cinereoargenteus*) in Southern California. Southwest Nat 57:176–181.
- Feltz CJ, Miller GE. 1996. An asymptotic test for the equality of coefficients of variation from k populations. Stat Med 15:647–658.
- Foster JB. 1964. Evolution of mammals on islands. Nature 202:234–235.
- Fritzell EK, Haroldson KJ. 1982. *Urocyon cinereoargenteus*. Mammal Species 189:1–8.
- Gaston KJ, Lawton JH. 1988. Patterns in body size, population dynamics, and regional distribution of bracken herbivores. Am Nat 132:662–680.
- Gittelman JL. 1985. Body size: ecological and taxonomic correlates. Acta Oecol 67:540–554.
- Gordon AD, Nevell L, Wood B. 2008. The *Homo floresiensis* cranium (LB1): size, scaling, and early *Homo* affinities. PNAS USA 105:4650–4655.
- Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. Biol Rev 41:587–640.
- Gould SJ. 1971. Geometric similarity in allometric growth: a contribution to the problem of scaling in the evolution of size. Am Nat 105:113–134.
- Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Bio Sci 205:581–598.
- Harris MA, Steudel K. 1997. Ecological correlates of hind-limb length in the Carnivora. J Zool 241:381–408.
- Henneberg M, Eckhardt RB, Chavanaves S, Hsü KJ. 2014. Evolved developmental homeostasis disturbed in LB1 from Flores, Indonesia, denotes Down syndrome and not diagnostic traits of the invalid species *Homo floresiensis*. PNAS Sciences USA 111:11967–11972.

Hershkovitz I, Kornreich L, Laron Z. 2007. Comparative skeletal features between *Homo floresiensis* and patients with primary growth hormone insensitivity (Laron Syndrome). Am J Phys Anth 134:198–208.

Hofman BR, Garcelon DK. 2010. Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator. Acta Oecol 165:699–705.

Hofman CA, Rick TC, Hawkins MTR, Funk WC, Ralls K, Boser CL, Collins PW, Coonan T, King JL, Morrison SA, Newsome SD, Sillett TS, Fleischer RC, Maldonado JE. 2015. Mitochondrial genomes suggest rapid evolution of Dwarf California Channel Islands Foxes (*Urocyon littoralis*). PLoS One 10:e0118240.

Hofman CA, Rick TC, Laldonado JE, Collins PW, Erlandson JM, Fleischer RC, Smith C, Sillett TS, Ralls K, Teeter W, Vellanoweth R, Newsome SD. 2016. Tracking the origins and diet of an endemic island canid (*Urocyon littoralis*) across 7300 years of human cultural and environmental change. J Quaternary Sci 146:147–160.

Holliday TW. 2012. Body size, body shape, and the circumscription of the genus *Homo*. Curr Anthro 53:S330–S345.

Holliday TW, Franciscus RG. 2009. Body size and its consequences: allometry and the lower limb length of Liang Bua 1 (*Homo floresiensis*). J Hum Evo 57:223–228.

Holliday TW, Franciscus RG. 2012. Humeral length allometry in African hominids (sensu lato) with special reference to AL 288-1 and Liang Bua 1. PaleoAnthro 1–12.

Holliday TW, Churchill SE, Carlson KJ, DeSilva JM, Schmid P, Walker CS, Berger LR. 2018. Body size and proportions of *Australopithecus sediba*. PaleoAnthro 406–422.

- Hudgens BR, Garcelon DK. 2011. Induced changes in island fox (*Urocyon littoralis*) activity do not mitigate the extinction threat posed by a novel predator. *Acta Oecol* 165:699–705.
- Illius AW, Gordon IJ. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Acta Oecol* 9:428–434.
- Jolicoeur P. 1975. Linear regression in fishery research: some comments. *J Fish Res Board Can* 32:1491–1494.
- Jungers WL. 2009. Interlimb proportions in humans and fossil hominins: variability and scaling. In: Grine FE, Fleagle JG, Leakey RE. (Eds.), *The First Humans: Origins and Early Evolution of the Genus Homo*. Springer, London, 93–98.
- Jungers WL, Harcourt-Smith WEH, Wunderlich RE, Tocheri MW, Larson SG, Sutikna T, Due RA, Morwood MJ. 2009a. The foot of *Homo floresiensis*. *Nature* 459:81–84.
- Jungers WL, Kaifu Y. 2011. On dental wear, dental work, and oral health in the type specimen (LB1) of *Homo floresiensis*. *Am J Phys Anth* 145:282–289.
- Jungers WL, Larson SG, Harcourt-Smith W, Morwood MJ, Sutikna T, Due RA, Djubiantono T. 2009b. Descriptions of the lower limb skeleton of *Homo floresiensis*. *J Hum Evo* 57:538–554.
- Kaifu Y, Baba H, Sutikna T, Morwood MJ, Kubo D, Saptomo EW, Jatmiko, Due RA, Djubiantono T. 2011. Craniofacial morphology of *Homo floresiensis*: description, taxonomic affinities, and evolutionary implication. *J Hum Evo* 61:644–682.
- Kaifu Y, Kono RT, Sutikna T, Saptomo EW, Due RA, Baba H. 2015. Descriptions of the dental remains of *Homo floresiensis*. *J Anthro Sci* 123:129–145.
- Kitchener AC, Beaumont MA, Richardson D. 2006. Geographical variation in the clouded leopard, *Neofelis nebulosa*, reveals two species. *Curr Biol* 16:2377–2383.

- Kościński K, Pietraszewski S. 2004. Methods to estimate sexual dimorphism from unsexed samples: a test with computer-generated samples. *Anthropol Rev* 67:33–55.
- Larick R, Ciochon RL, Zaim Y, Rizal Y, Aziz F, Reagan M, Heizler M. 2001. Early Pleistocene 40Ar/39Ar ages for Bapang formation hominins, central Jawa, Indonesia. *PNAS USA* 98:4866–4871.
- Larramendi A. 2016. Shoulder height, body mass, and shape of proboscideans. *Acta Palaeontol Polonica* 61:537–574.
- Larson SG, Jungers WL, Tocheri MW, Orr CM, Morwood MJ, Sutikna T, Due RA, Djubiantono T. 2009. Descriptions of the upper limb skeleton of *Homo floresiensis*. *J Hum Evo* 57:555–570.
- Larson SG, Jungers WL, Morwood MJ, Sutikna T, Sapitomo EW, Due RA, Djubiantono T. 2006. *Homo floresiensis* and the evolution of the hominin shoulder. *J Hum Evo* 53:718–731.
- Leinders JJM, Sondaar PY. 1974. On functional fusions in footbones of Ungulates. *Zeitschrift fur Säugetierkunde* 39:109–115.
- Lieberman DE. 2009. *Homo floresiensis* from head to toe. *Nature* 459:41–42.
- Lomolino MV. 2005. Body size evolution in insular vertebrates: generality of the island rule. *J Biogeogr* 32:1683 –1699.
- Lomolino MV, Sax DF, Palombo MR, van der Geer AA. 2012. Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. *J Biogeogr* 39:842–854.
- Lytras G, Dermitzakis MD, van der Geer AA, van der Geer SB, De Vos J. 2009. The origin of *Homo floresiensis* and its relation to evolutionary processes under isolation. *J Anthropol Sci* 117:33–43.

- Lyras G, van der Geer AA. 2006. Adaptations of the Pleistocene island canid *Cynotherium sardous* (Sardinia, Italy) for hunting small prey. *Cranium* 23:51–60.
- Marshall LG, Corruccini RS. 1978. Variability, evolutionary rates, and allometry in dwarfing lineages. *Paleobiol* 4:101–119.
- Martin RD, MacLarnon AM, Phillips JL, Dussubieux L, Williams PR, Dobyns WB. 2006. Comment on “The brain of LB1 *Homo floresiensis*.” *Science* 312:999.
- Maynard-Smith J, Burian R, Kauffman S, Alberch R, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L. 1985. Developmental constraints and evolution: a perspective from the mountain lake conference on development and evolution. *Quart Rev Biol* 60:265–287.
- Mayr E. 1946. Systematics and the origin of species. Columbia University Press, New York.
- Mazák JH, Groves C.P. 2006. A taxonomic revision of the tigers (*Panthera tigris*) of Southeast Asia. *Mammal Biol* 71:268–287.
- Mazák V. 1981. *Panthera tigris*. *Mammal Biol* 152:1–8.
- McFadden KW, Meiri S. 2013. Dwarfism in insular carnivores: a case study of the pygmy raccoon. *J Zool* 289:213–221.
- McFadden KW, Sambrotto RN, Medellín R, Gompper ME. 2006. Feeding habits of endangered pygmy raccoons (*Procyon pygmaeus*) based on stable isotope and fecal analyses. *J Mammal* 87:501–509.
- Meachen-Samuels J, Van Valkenburgh J. 2009. Forelimb indicators of prey-size preference in the Felidae. *J Morpho* 270:729–744.
- Merriam CH. 1901. Six new mammals from Cozumel Island, Yucatan. *Proc Biol Soc Wash* 14:99–104.

- Montgomery S, Capellini I, Barton R, Mundy NI. 2010. Reconstructing the ups and downs of primate brain evolution: implications for adaptive hypotheses and *Homo floresiensis*. *BMC Biol* 8:1–19.
- Moore CM, Collins PW. 1995. *Urocyon littoralis*. *Mammal Spec* 489:1–7.
- Morley MW, Goldberg P, Sutikna T, Tocheri MW, Prinsloo LC, Jatmiko, Sapomo EW, Wasisto S, Roberts RG. 2017. Initial micromorphological results from Liang Bua, Flores (Indonesia): site formation processes and hominin activities at the type locality of *Homo floresiensis*. *J Archaeol Sci* 77:125–142.
- Morse DH. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Mass.
- Morwood MJ, O’Sullivan P, Susanto EE, Aziz F. 2003. Revised age for Mojokerto 1, an early *Homo erectus* cranium from East Java, Indonesia. *Aus Archaeol* 57:1–4.
- Newell ND. 1949. Phyletic size increase, an important trend illustrated by fossil invertebrates. *Evolution* 3:103–124.
- Palombo MR. 2001. Paedomorphic features and allometric growth in the skull of *Elephas falconeri* from Spinagallo (Middle Pleistocene, Sicily). In: Cavarretta G, Gioia P, Mussi M, Palombo MR (Eds.), *The World of Elephants. Proceedings of the First International Congress*. Consiglio Nazionale delle Richerche, Rome, 492–496.
- Pébalon C, Bolstad GH, Egset CK, Cheverud JM, Pavlicev M, Rosenqvist G. 2013. On the relationship between ontogenetic and static allometry. *Am Nat* 181:195–211.
- Plavcan JM. 1994. Comparison of four simple methods for estimating sexual dimorphism in fossils. *Am J Phys Anth* 94:465–476.
- Polk JD. 2004. Influences of limb proportions and body size on locomotor kinematics in terrestrial primates and fossil hominins. *J Hum Evo* 47:237–252.

- Pontzer H. 2007. Effective limb length and the scaling of locomotor cost in terrestrial mammals. *J Exp Biol* 210:1752–1761.
- Prothero DR, Sereno PC. 1982. Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. *Paleobiol* 8:16–30.
- Puspanigrum M, Van Den Bergh G, Chivas A, Setiabudi E, Kurniawan I. 2014. Preliminary results of dietary and environmental reconstructions of Early to Middle Pleistocene Stegodons from the So'a Basin of Flores, Indonesia, based on enamel stable isotope records. *Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Greece. VIth international Conference on Mastodons and their Relatives, Grevena–Siatista. Special Volume* 102:164–165.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Raia P, Meiri S. 2006. The island rule in large mammals: paleontology meets ecology. *Evolution* 60:1731–1742.
- Richards GD. 2006. Genetic, physiologic and ecogeographic factors contributing to variation in *Homo sapiens*: *Homo floresiensis* reconsidered. *J Evol Biol* 19:1744–1767.
- Rick TC, Erlandson JM, Vellanoweth RL, Braje TJ, Collins PW, Guthrie DA, Stafford Jr TW. 2009. Origins and antiquity of the island fox (*Urocyon littoralis*) on California's Channel Islands. *Quatern Res* 71:93–98.
- Rizal Y, Westaway KE, Zaim Y, van den Bergh GD, Arthur BW, Morwood MJ, Huffman OF, Grün R, Joannes-Boyau R, Bailey RM, Westaway MC. 2020. Last appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. *Nature* 577:381–385.

Roehmer GW, Smith DA, Garcelon DK, Wayne RK. 2001. The behavioural ecology of the island fox (*Urocyon littoralis*). *J Zool* 255:1–14.

Rosenzweig ML. 1966. Community structure in sympatric carnivores. *J Mammal* 47: 602–620.

Roth VL. 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. *Oxford Surv Evol Biol* 8:259.

Rubin CL, Lanyon LE. 1984. Dynamic strain similarity in vertebrates; an alternative to allometric limb bone scaling. *J Theor Biol* 107:321–327.

Schoenemann PT, Allen JS. 2006. Scaling of brain and body weight within modern and fossil hominids: implications for the Flores specimen. *Am J Phys Anth* 129:59–60.

Schutz H, Polly PD, Krieger JD, Guralnick RP. 2009. Differential sexual dimorphism: size and shape in the cranium and pelvis of grey foxes (*Urocyon*). *Biol J Linn Soc* 96:339–353.

Shea BT, Gomez AM. 1988. Tooth scaling and evolutionary dwarfism: an investigation of allometry in human pygmies. *Am J Phys Anth* 77:117–132.

Singer MS, Bernays EA. 2003. Understanding omnivory needs a behavioral perspective. *Ecology* 84:2532–2537.

Smith RJ. 2009. Use and misuse of the reduced major axis for line-fitting. *Am J Phys Anth* 140:476–486.

Sondaar PY. 1977. Insularity and its effect on mammal evolution. In: Goody PC, Hecht BM, Hechtieds MK (Eds.), *Major Patterns in Vertebrate Evolution*. Springer, Boston, 671–707.

- Sondaar PY, Boekschoten GJ. 1967. Quaternary mammals in the South Aegean island arc with notes on other mammals from the coastal regions of the Mediterranean, I/II. Proc Kon Ned Akad Wetensch Series B 70:556–576.
- Stanley SM. 1979. Macroevolution, Pattern and Process. John Hopkins University Press.
- Sutikna T, Tocheri MW, Morwood MJ, Saptomo EW, Due RA, Wasisto S, Westaway KW, Aubert M, Li B, Zhao JX, Storey M. 2014. Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. Nature 532:366–369.
- Szabó K, Amesbury JR. 2011. Molluscs in a world of islands: the use of shellfish as a food resource in tropical island Asia-Pacific region. Quatern Int 239:8–18.
- Tocheri MW, Orr CM, Larson SG, Sutikna T, Jatmiko, Saptomo EW, Due RA, Djubiantono T, Morwood MJ, Jungers WL. 2007. The primitive wrist of *Homo floresiensis* and its implications for hominin evolution. Science 317:1743–1745.
- van den Bergh GD, Meijer HJ, Due RA, Morwood MJ, Szabo K, van den Hoek, Ostende LW, Sutikna T, Saptomo EW, Piper PJ, Dobney KM. 2009. The Liang Bua faunal remains: a 95k.yr. sequence from Flores, East Indonesia. J Hum Evo 57:527–537.
- van den Bergh GD, Kaifu Y, Kurniawan I, Kono RT, Brumm A, Setiyabudi E, Aziz F, Morwood MJ. 2016. *Homo floresiensis*-like fossils from the early Middle Pleistocene of Flores. Nature 534:245–248.
- van der Geer AA. 2005. Island ruminants and parallel evolution of functional structures. In: Crégut-Bonouure E (Ed.), Les ongulés holarctiques du Pliocène et du Pléistocene. Quaternaire, Int J French Quater Ass, hors-série 2:241–256. Paris: Maison de la Géologie.
- van der Geer AA. 2014. Parallel patterns and trends in functional structures in extinct island mammals. Integr Zool 9:167–182.

Wayne RK. 1986. Limb morphology of domestic and wild canids: the influence of development on morphologic change. *J Morpho* 187:301–319.

Wayne RK, George SB, Gilbert D, Collins PW, Kovach SD, Girman D, Lehman N. 1991. A morphologic and genetic study of the island fox, *Urocyon littoralis*. *Evolution* 45:1849–1868.

Weston EM, Lister AM. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. *Nature* 459:85–88.

White JF, Gould SJ. 1965. Interpretation of the coefficient in the allometric equation. *Am Nat* 99:5–18.

Zar JH. 1968. Calculation and miscalculation of the allometric equation as a model in biological data. *Biosci* 18:1118–1120.

**CHAPTER 4:**  
**BODY SIZE, SHAPE, AND ROBUSTICITY IN A DESERT PENINSULA**  
**POPULATION: BIOLOGICAL AND BEHAVIORAL RESPONSES TO HEAT**  
**AND ARIDITY IN THE HOLOCENE OF BAJA CALIFORNIA SUR**

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## **Abstract**

Baja California is the second longest peninsula in the world, characterized by 1000 km of hot desert circumscribed by ocean, and has been occupied by human populations throughout the Holocene. Here, we measured body size, shape, and robusticity of Middle to Late Holocene human skeletal remains in two regions in Baja California, the Central Desert Sierras and the Cape Region, to understand the interplay among behavioral dynamics around finite resources and human body form for peninsular marine-hunter-gatherers. Based on previous analyses, we predict that Baja California populations will show ecogeographic body proportions similar to other hot and arid adapted groups, but distinct patterns of postcranial robusticity corresponding with differences in maritime adaptations. We compared brachial and crural indices, stature, body mass, and bi-iliac breadth to nearby Amerindian and similar latitudinal humans. Further, we compared long bone cross-sectional properties to a diverse sample of humans from varying subsistence and ecogeographic contexts. We found biological responses to heat are present in the Cape Region while responses to heat and aridity are in the Central Desert Sierras. Further, we identified markedly different loading patterns suggesting diverse community-resource dynamics. Individuals in the Cape Region likely experienced elevated isolation, and greater access to environmental resources, resulting in a heat-adapted body with a high body mass. Individuals in the Central Desert Sierras had less convenient access to oceanic and freshwater resources resulting in a heat-adapted body with lower stature and body mass.

## **Keywords**

Ecogeographic body proportions, body size, robusticity, cross-sectional geometry, marine-hunter-gatherers, coastal adaptations, Baja California prehistory

## **Introduction**

Humans are remarkable for their ability to colonize novel habitats, including extreme ecosystems that present considerable challenges to growth and survival through stressful climates and limited resources. The Baja California peninsula, the world's second longest peninsula, is such an environment, where extreme heat and freshwater scarcity represent considerable challenges to human survival and wellbeing. Despite its connection to populated areas in North America, Baja California is commonly noted as one of the most isolated regions in the world, likely because it is an elongated hot desert circumscribed by the Sea of Cortéz on the east and the Pacific Ocean on the west, making access extremely difficult (Baegert, 1952; Krutch, 1961; Aschmann, 1967; Guillén, 1979; del Barco, 1980; Berger, 1998). Roughly two-thirds of the peninsula (~1000 km) is classified as a hot desert (BWh, Koppen-Geiger climate classification) with an average temperature of 32 °C and scant precipitation, averaging 15 cm annually. Consequently, despite the massive length of the peninsula (~1600 km), the only permanent source of surficial freshwater exists as arid land springs which emerge sporadically throughout its length (Maya et al., 1997). Modern floral distributions were likely established around 4,000 years ago, but the peninsula has experienced the same basic hot and dry climate for the last 7500 years (Van Devender, 1994; Barron et al., 2012) and tree ring data corroborate this for the last several hundred years (Diaz et al., 2001). This research will

evaluate biological and behavioral responses to heat and aridity in two human populations who lived in the peninsula during the Holocene.

Humans dynamically survived in this region for most of the Holocene in distinct cultural-linguistic groups and at contact were generally patterned in a north to south cline down the peninsula as: Yuman speaking groups in the north, Proto-Yuman speaking Cochimi in the Central Desert, Guaycura in the Magdalena Plains, and the Pericú in the southern Cape Region (Massey, 1947; Mixco, 2006; Laylander and Moore, 2006). Two regions, in particular, demonstrate remarkable contrasts in human behavioral dynamics: the Central Desert and the Cape Region. Early descriptions of human skeletal remains from the Cape Region highlight possible regional biological variation (ten Kate, 1884; Diguet, 1905; Rivet, 1909; Tyson, 1977), but a lack of human skeletal remains from the Central Desert has resulted in a dearth of information on the paleobiology of this region (but see Tyson, 1975). The Cape Region was described as having tall and robust individuals with high intralimb indices and hyperdolicocephalic crania, which are unique traits compared to other nearby Amerindian groups, leading early researchers to suggest a Melanesian or Andaman Islands origin (Baegert, 1952; Tyson, 1977).

The Cape Region was initially colonized by North American Amerindians during the Terminal Pleistocene via a coastal route and was likely inhabited for the entire Holocene (González-José et al., 2003; Fujita, 2006; Raghavan et al., 2015; Des Laurers et al., 2017; Fujita and Ainis, 2018). It is an isolated ecoregion on the southern tip of the peninsula, and acts as an oasis in the primarily hot desert, where slightly increased annual precipitation (~30 cm) differentiate its climate as hot semi-arid (BSh). Groups organized themselves in residential camps around the Sierra de la Laguna in a way that provided

access to freshwater springs in the mountains and marine resources on the coast, similar to Hawaiian's practice of "ahupua'a" (Figure 1; Weisler and Kirch, 1985; Fujita, 2006). They navigated the nearby ocean as excellent sea voyagers, using log rafts and spears for pelagic resources and to travel among local islands (Napolí, 1721; Clavijero, 1937; Baegert, 1952; Heizer and Massey, 1953; Massey, 1966; Fujita, 1995). Faunal analyses support a unique maritime adaptation with increased reliance on dolphins and oysters in conjunction with nearshore shellfish (Porcasi and Fujita, 2000; Fujita and Minagawa, 2004; Fujita, 2006; Ainis et al., 2019). Humans supplemented their marine diet with terrestrial resources including sweet pitahaya, cardón, and prickly pear, and used the atlatl to hunt deer and sheep (Massey, 1947, 1961, 1966). Carbon and Nitrogen isotopes from human skeletal remains support increased reliance on marine resources relative to terrestrial foods (Molto and Kennedy, 1991; King, 1997; Fujita and Minagawa, 2004).

Later, Early Holocene migrations from the American Southwest and Great Basin areas brought humans into the Central Desert who differed from those in the Cape Region (Hyland and Gutiérrez-Martínez, 1995; Ritter, 2006; Gutiérrez-Martínez, 2019). The Central Desert is a hot desert with bi-annual precipitation (~15 cm annually) influenced by the North American Monsoon seasons resulting in periods of food and water shortages and significant dietary stress (Viscaíno, 1596; de la Ascensión, 1602; Napolí, 1721; Venegas, 1759; Clavijero, 1937; Baegert, 1952; Sales, 1956; de Salvatierra, 1971; del Barco, 1973, 1980, 1981; Touhy, 1978). Humans navigated this landscape in small, logically mobile foraging units that traversed the desert in an east-west cline, navigating around freshwater springs (Figure 1; Baegert, 1952; Aschmann, 1967; Tyson, 1975; Ritter, 1979; Henrickson, 2013; Guitérrez-Martínez, 2019). Increased contact with

northern groups was likely beneficial during periods of shortage (Aschmann, 1967; Tyson, 1975) and the introduction of the bow and arrow in the Late Holocene likely represents this contact (Hyland and Gutiérrez, 1995; Hyland, 2006). They primarily subsisted on mesquite beans, small grass, agave root, fish, shellfish, seeds, rabbit, deer, sheep, antelope, and lizards (Aschmann, 1967; Mathes, 2006). While the Cochimi in this region used bolsa boats for some marine procurement they were noted as being less adept with marine livelihoods, compared to other groups (Wagner, 1929; Heizer and Massey, 1953). Carbon and Nitrogen isotopes indicate regional diversification of subsistence strategies with increased reliance on terrestrial resources at inland sites (King, 1997).

When inhabiting a hot desert environment, humans are confronted with the risks of heat stress and dehydration (Moran, 2008; Hora et al., 2020), and selective pressures related to these stressors may result in changes to body size and shape (Ruff, 2002). Global patterns of human variation indicate that human populations inhabiting hot environments broadly conform to ecogeographic predictions of Allen (1887) and Bergmann's (1847) rules. Specifically, they display narrow bi-illiac breadths, elongate limbs, and relatively long distal limb extremities, which result in overall high ratios of surface area to volume that effectively dissipate heat (Robinson, 1968; Trinkaus, 1981; Ruff and Walker, 1993; Holliday, 1997a,b). However, while increased sweating can act to cool the body in hot-arid environments, in areas with scarce freshwater, dehydration is then an added high risk (Hora et al., 2020). Smaller body masses may act to reduce water needs and be an advantage for humans in arid environments (Bethancourt et al., 2020), and in conjunction with stature reduction, be a response to periods of nutritional stress related to water scarcity or droughts (Eveleth and Tanner, 1976; Tanner et al., 1982; Shea

and Bailey, 1996; Bogin et al., 2002; Kuzawa and Bragg, 2012). Human groups with long-term occupations in hot-arid regions display body size and shape that likely represent a local adaptive response to negotiate these challenges (Ruff, 1994, 2002; Holliday, 1997; Cowgill et al., 2012).

Local adaptation to ecogeographic pressures is also significantly influenced by population structure resulting in variation in the patterning and timing of body size and shape responses (Holliday, 1997; Roseman and Auerbach, 2015). Holistic analyses of North American Amerindians identified a body size and shape that is generally characterized as cold-adapted (Auerbach, 2012). While intralimb indices varied among individuals, bi-iliac breadth was consistently wider compared to global samples. This trend is apparent in the Early and Late Holocene samples suggesting that a prolong period of isolation in Beringia prior to North American colonization reduced the variation in this trait, constraining body size and shape responses to ecogeographic variables in North America. Amerindians in Baja California were closely related to Early Holocene Amerindians who migrated through Beringia (Raghavan et al., 2015; Des Laurers et al., 2017; Fujita and Ainis, 2018). Long-term occupation of this Amerindian body type in a peninsular hot-arid ecology may result in a body type that is divergent from similar latitudinal groups with distinct population structures.

Additionally, humans in coastal areas with maritime adaptations may successfully navigate around finite terrestrial resources (Erlandson and Fitzpatrick, 2006; Kirch and Green, 1987; Kirch, 1986; Des Lauries, 2010). While ethnohistoric and archaeological data offer clues on how humans were behaviorally responding to the Baja California peninsula in the past, analyses of cross-sectional geometric properties provide a valuable

insight into habitual behaviors and subsistence strategies (Ruff and Hayes, 1983a, 1983b; Ruff and Larsen, 2014). Because bone responds to strain by adding and removing bone and changing shape, measuring the amount and distribution of bone within a cross-section has shed light on mobility, weapons use, resource procurement, terrain, and sexual division of labor (Ruff et al., 1984, 1993, 2006; Ruff, 1987, 2019; Bridges, 1989, 2000, 2005; Trinkaus et al., 1994; Stock and Pfeiffer, 2001, 2004; Weiss, 2003; Wescott and Cunningham, 2006; Marchi, 2008; Maggiano et al., 2008; Ogilvie and Hilton, 2011; Watson and Stoll, 2013; Davies and Stock, 2014).

Analyses of cross-sectional geometry has successfully detected population differences related to terrain type, including differences between terrestrial and water transport. Increases in cross-sectional areas and second moments of area are associated with increased loading intensity in active and mobile individuals, but also in groups who inhabit areas with rugged terrain (Ruff, 1987; Weiss, 2003; Wescott, 2006; Marchi, 2008; Ruff, 2019; Temple et al., 2021). Individuals who navigate rugged oceanic or mountainous terrain have humeral, femoral, and tibial midshaft cross-sections with elevated bone mass and torsional rigidity compared to groups who traverse flat aquatic or terrestrial terrain (Weiss, 2003; Bridges, 2005; Marchi, 2008). The effect of terrain is also reflected in the shape values ( $I_{max}/I_{min}$ ) of humeral and lower limb diaphyseal shafts. Individuals involved in oceanic verses river rowing will have increased circularity (decreased  $I_{max}/I_{min}$ ) of 50% humeral sections (Stock and Pfeiffer, 2001; Shaw and Stock, 2009). This is in contrast to lower limb shape ratios, where individuals who are active over rugged terrain will have decreased circularity and increased anterior-posterior

reinforcement of femoral and tibial midshaft diaphyseal sections compared to those with less intense mobility (Ruff and Hayes, 1983a; Marchi, 2008).

The types of activity also influence levels of upper and lower limb cross-sectional asymmetry. Marine-hunter-gatherers who depend on benthic and pelagic marine resources show greater humeral robusticity compared to non-marine hunter-gatherers (Stock and Pfeiffer, 2001; Weiss, 2003). Males tend to have the highest levels of total area and torsional rigidity which is associated with increased watercraft use and swimming (Weiss, 2003; Shaw and Stock, 2009). Females who predominately gather shellfish, use digging sticks, and procure food with mortar and pestle have decreased robusticity and circularity compared to males in their humeral cross-sections due to increased habitual loadings in one plane (Stock and Pfeiffer, 2004). High levels of humeral asymmetry is also apparent in men who use the atlatl and in females who habitually gather shellfish (Trinkaus et al., 1994; Stock and Pfeiffer, 2004).

To better understand aspects of biological diversity of pre-conquest individuals in the Baja California peninsula, we evaluate body size, shape, and patterns of robusticity in response to heat, aridity, and potential exploitation of maritime resources. In doing so, we contribute to the growing literature on the impacts that increased temperatures and aridity have on human diversity (Cremaschi and Di Lernia, 1999; Santoro et al., 2016; Bethancourt et al., 2020; Hora et al., 2020; Pontzer et al., 2021). To do so, this research will evaluate how body mass, stature, bi-iliac breadth, and intramembral proportions differ for two groups in the Cape Region and Central Desert in southern Baja California compared to nearby Amerindians and latitudinally similar non-industrialized humans. Second, we evaluate how humeral and lower limb robusticity are patterned for these

groups and whether they reflect what archaeological and ethnohistoric data suggest about their behavioral dynamics in this region.

## **Materials and Methods**

### *Sample*

#### Cape Region

Human skeletal remains (n=29) were analyzed from five archaeological sites from the Cape Region located at about 24 °N, which are located at the base of the Sierra de la Laguna (2,090 m): Agua Amarga, Cabo Pulmo, Los Frailes, Piedra Gorda, and Punta Pescadero ; (Figure 1). They represent burials from four mortuary caves and one open site (Massey, 1947; Tyson, 1977; Pompa, 2018). Many of the burials are of the Las Palmas burial tradition represented by secondary bundled burials with red ochre staining (Massey, 1955). Dating of the palm bark and braid at Cabo Pulmo places the remains at 1320 to 1420 ca AD (Tyson, 1977). Carbon isotopes from Piedra Gorda and Punta Pescadero indicate similar Late Holocene 1400-1600 ca AD occupation (Molto and Kennedy, 1991). Periostitis with diaphyseal inflammation and osteoblastic responses were identified on three tibiae, one humerus, and one femur. These elements were excluded from cross-sectional geometric analyses.

#### Central Desert

Human skeletal remains (n=6) were sampled from the southern portion of the Central Desert from La Gallineta and Cueva de los Muertos archaeological sites located at about 26 °N in the Sierra de Guadalupe of the Central Desert Sierras (Figure 1). Sierra de Guadalupe reaches up to 1700 m and has increased freshwater springs compared to the coast (de Alba, 2021; Cariño, 2021). Carbon isotopes analyzed from four skeletal

samples at La Gallineta produced radiocarbon dates for the Middle Holocene at ca BC 966-671. Five skeletal samples from Cueva de los Muertos produced radiocarbon dates also for the Middle Holocene at ca BC 974-846 and ca BC 69-18 AD (Gutiérrez Martínez, pers. comm.). Post-interment burning and cremation was present on the skeletal remains, which was a common burial practice marking the Comondú tradition associated with the southern Cochimi (Ritter, 2006; Gutiérrez Martínez, 2019; Fujita, pers. comm.).

#### Comparative samples

To identify whether the body size and proportions of these groups are similar to nearby Amerindians or similar-latitudinal groups, comparative samples were chosen from the Goldman Osteological dataset (Auerbach and Ruff, 2004; Auerbach, 2012; Table 1). Nearby Amerindians are represented by pre-conquest groups from Arizona and New Mexico. These samples were chosen because of their geographic proximity and purported occasional trade with northern and central Baja California groups (Aschmann, 1967). Similar latitudinal groups are of pre-conquest individuals with long-term occupations in hot semi-arid and arid climates from latitudes between 23 – 26 °N/S and are represented by Australia and Egypt (Table 1).

To make inferences on the types and intensity of activity of individuals from the Cape Region and Central Desert Sierras, cross-sectional geometric properties of the humerus, femur, and tibia were compared to a diverse sample of non-industrial humans who differed in behaviors (marine-hunter-gatherers to agriculturalists) and terrain (Table 1). Alaska North Coast, Alaska Coast, and Andaman Island samples represent individuals with high levels of maritime adaptations with varying degrees of marine hunting,

watercraft use, swimming, and shellfish gathering (Table 1; Stock and Pfeiffer, 2001; Stock, 2006; Temple et al., 2021). Alaska Coast and Andaman Island are of individuals with low levels of terrestrial mobility in relatively flatter terrain, while Alaska North Coast is characterized by individuals with high levels of activity in both rugged oceanic and mountainous terrestrial terrain. Alaska River samples represent semi-sedentary hunter-gatherers in a rugged terrain, while Pecos Pueblo are of sedentary agriculturalists with logistical hunting and foraging in rugged terrain (Table 1; Ruff and Hayes, 1983a,b; Temple et al., 2021).

## Analysis

The focus of this analysis is on the body size, shape, and robusticity of pre-contact adult (> 18 years old) Amerindians in the Central Desert Sierras and Cape Region. Age of adults was identified using the pubic symphysis (Brooks and Suchey, 1990), auricular surface (Lovejoy et al., 1985), cranial suture closure (Meindl and Lovejoy, 1985), and dental wear (Lovejoy, 1985). Sex of adults was identified using features of the os coxae and skull (Buikstra and Ubelaker, 1994; Ubelaker, 1999).

In order to characterize body proportions, limb indices, and stature, maximum lengths of the humerus, radius, femur, and tibia were measured to the nearest 0.5 mm, and bi-iliac breadth was measured to the nearest 0.5 mm using spreading calipers. Bi-iliac breadth was not available for the Central Desert Sierras due to poor preservation. Femoral head superior-inferior diameter was measured to the nearest 0.01 mm using handheld digital calipers to estimate body mass. Body mass was estimated using femoral head diameter and the average of Ruff et al. (1991), McHenry (1992), and Grine et al. (1995)

equations. Stature was estimated for individuals from Baja California, Arizona, and New Mexico using maximum lengths of the femur and the revised Genovés (1967) Mesoamerican femoral equations from del Angel and Cisneros (2004). These equations were originally calculated from 235 Mesoamerican cadavers (Genovés, 1967) and recently updated by del Angel and Cisneros (2004) due to minor estimation errors, and are recommended for Southwest and Mesoamerican Amerindian stature estimation (Auerbach and Ruff, 2010). Equations derived from appropriate reference samples based on limb proportions were used to estimate stature in Australia and Egypt skeletal remains (Auerbach and Ruff, 2004). For Australia, maximum length of the tibia was used following Allbrook (1961) equations that were calculated from Nilohamite and recommended for Australians due to their crural indices being most similar to East Africans compared to other reference samples (Auerbach and Ruff, 2004). Egyptian stature was calculated using maximum femur length and the average of the “white” and “black” formulae of Trotter and Gleser (1952) following (Holliday, 2002) and Auerbach and Ruff (2004). Sex-specific stature estimations were used when appropriate and when sex was known, but if sex was unknown, the average of the male and female estimations was taken.

#### *Cross-sectional geometric data*

We assessed the cross-sectional properties of bilateral humeri and unilateral femora and tibiae using subperiosteal molds (O’Neill and Ruff, 2004). Humeral, femoral, and tibial 50% sections were determined via 50% of biomechanical length. Total area (TA), second polar moments of area ( $I_{max}$  and  $I_{min}$ ), and the polar moment of area (J) were

calculated using BoneJ and SLICE in ImageJ via external diaphyseal subperiosteal molds. Total area corresponds to the total area of the section,  $I_{max}$  and  $I_{min}$  represent maximum and minimum bending rigidity, and  $J$  is a proxy for average or torsional rigidity.

Field limitations prevented the use of biplanar radiography or CT scans for the reconstruction of endosteal contours, so external diaphyseal dimensions via subperiosteal molds were used to estimate true diaphyseal dimensions. Multiple analyses have confirmed that there is a high correspondence between solid sections reconstructed with molds and “true” values evaluated via CT scan (Wescott, 2006; Wescott and Cunningham, 2006; Stock and Shaw, 2007; Sparacello and Pearson, 2010; Macintosh et al., 2013). Regressions of solid  $I_{max}/I_{min}$  (without medullary cavities) against true  $I_{max}/I_{min}$  (with medullary cavities) and solid  $J$  against true  $J$  have  $r^2$  values greater than 0.98 for the humerus, femur, and tibia (Sparacello and Pearson, 2010; Macintosh et al., 2013). Solid  $J$  and solid  $I_{max}/I_{min}$  were used to estimate true  $J$  and true  $I_{max}/I_{min}$  following the regression equations for 50% humerus, femur, and tibia in Macintosh et al. (2013).

To control for the effects of body size on diaphyses, ordinary least square (OLS) regressions of the logged cross-sectional property regressed on a logged measure of body size were constructed to derive standardized residuals. Humeral total area was regressed on bone length<sup>3</sup>, and polar moment of area was regressed on bone length<sup>5.33</sup> (Ruff, 2008). Tibial and femoral total area were regressed off body mass; tibial and femoral polar moment of area were regressed off the product of body mass and bone length<sup>2</sup> (Ruff, 2019). Because the comparison of limbs within an individual inherently controls for body size, raw values of  $I_{max}/I_{min}$  were assessed. Additionally, raw values of humeral asymmetry

of TA and J were assessed following Trinkaus et al. (1994) as [((maximum – minimum)/minimum)\*100].

### *Statistical analyses*

To test for differences in body size, shape, and robusticity among groups, Mann-Whitney u test were administered with a Holm-Bonferroni correction. The Holm-Bonferroni is a powerful p-value adjustment that reduces the type I error rate and is preferred over Bonferroni as it also reduces the type II error rate. Differences were tested among Cape Region, Central Desert Sierras, nearby Amerindians, and similar-latitudinal groups for stature, body mass, bi-iliac breadth, brachial, and crural indices. Robusticity was assessed among Cape Region, Central Desert Sierras, and comparative samples of diverse activity and subsistence levels (Table 1) by testing for differences in TA and J standardized residuals and  $I_{max}/I_{min}$  shape ratio and humeral asymmetry ratio of TA and J.

Statistical tests for cross-sectional properties were administered first among groups with combined sexes and then among the separated male and females of each group to identify within and between group behavioral differences. Central Desert Sierras had too few sex-specific long bones to be included in the sex-separated statistical analyses and therefore were only analyzed in group-level comparisons. All statistical analyses were run in R (R Core Team, 2021) and were deemed significantly different if the *p*-value was less than 0.05. Given the conservative nature of Holm-Bonferroni post-hoc p-value corrections and small sample sizes of some of the comparisons, non-significant values that varied in remarkable ways (such as outside of the range of variation of other groups) were also discussed.

## **Results**

### *Body size and proportions*

Summary statistics of body size and shape of individuals from the Cape Region and Central Desert Sierras are depicted in Table 2 and boxplots in Figures 2. Results of the Mann-Whitney pairwise u tests with Holm-Bonferroni correction (Table 2) demonstrated that individuals from the Cape Region were significantly different in stature compared to all groups except for Arizona and Egypt, having the third highest stature after Egypt and Australia. Further, body mass is highest for the Cape Region compared to all groups but only reached significance with New Mexico and Australia. Bi-iliac breadth is significantly narrower for the Cape Region compared to both New Mexico and Arizona Amerindians, crural index is significantly higher for the Cape Region compared to all groups. Brachial index of the Cape Region was significantly higher compared to all groups except Arizona. Individuals from the Central Desert Sierras were only significantly different in a smaller stature compared to hunter-gatherers from Australia and Egypt but are characterized by low body masses and high intralimb indices compared to all samples.

### *Long bone robusticity and interpretation of habitual behavior*

Box plots of standardized residuals of cross-sectional properties of the humeri (Figures 3 and 4) indicate increased humeral robusticity for the Cape Region compared to other groups. Results of Mann-Whitney U tests with Holm-Bonferroni corrections (Table 3) were significant for the Cape Region right humerus TA and J values compared to all groups except for Alaska coast and north coast. Right humeral  $I_{\max}/I_{\min}$  was also

significantly higher than all groups except for Andaman Islanders and Alaska Coast, while left humeral  $I_{max}/I_{min}$  differed from all groups except Andaman Islanders.

These results were primarily driven by the significant differences of Cape Region female left humerus TA and J values (Table 5; Figure 5). Female skeletal remains from the Cape Region were higher in left humerus J values compared to all groups. Humeral 50%  $I_{max}/I_{min}$  values of male and females from the Cape Region were most similar to Andaman Islanders and Pecos Pueblos (Table 5). Right humerus  $I_{max}/I_{min}$  shape values were highest for females from the Cape Region compared to all other samples (Figure 6). Males had levels of humeral asymmetry most similar to Andaman and north coast Alaska, whereas females demonstrated a wide range of variation in asymmetry, though none of these comparisons reached significance (Figure 7; Table 6).

Results of analyses of the standardized residuals of cross-sectional properties of the lower limb of individuals from the Cape Region were significantly different for the femur and tibia TA values compared to all groups except for femur TA values of north coast Alaska (Table 3). The Cape region did not significantly differ in femur J values compared to any of the groups. Tibia J were significantly higher for the Cape Region compared to Andaman Islanders. The Cape Region had significantly greater femur  $I_{max}/I_{min}$  values compared to all groups, but significantly lower tibia  $I_{max}/I_{min}$  values compared to all groups except Alaska Coast.

Sex-specific comparisons of the lower limb indicated that males from the Cape Region had femur TA values greater than all other groups, but femur J values not significantly different than any groups. Femur  $I_{max}/I_{min}$  values were significantly lower for Cape Region males compared to all groups. Cape Region females had femur TA and J

values significantly greater than all groups except Pecos Pueblo and North Coast Alaska. Cape Region females only significantly differed in femur  $I_{max}/I_{min}$  compared to Alaska River and Alaska Coast.

Cape Region males had significantly greater tibia TA levels compared to all groups but did not significantly differ in tibia J levels (Table 5). Tibia  $I_{max}/I_{min}$  properties were different for Cape Region males who have greater shape values compared to all other males except for north coast Alaskans and Andaman Islanders (Table 5). Female tibia were only significant different from Alaska Coast, Alaska River, and Andaman Islanders in TA values, and had significantly lower tibia  $I_{max}/I_{min}$  compared to Pecos Pueblo. Tibia shape values were generally low for male and females but only reached significance in comparison to Pecos Pueblo.

Individuals from the Central Desert Sierras had distinct humeral and lower limb robusticity properties compared to the other groups that indicated patterns of behavior that resulted in greater lower limb loading compared to the upper limb. Right humerus TA and J were significantly lower compared to Andaman Islanders and Pecos Pueblo. The Central Desert Sierras were outside of the range of variation of most other groups and had significantly higher right humerus  $I_{max}/I_{min}$  values compared to Andaman Islanders and Pecos Pueblo (Figure 4). They had femora with high  $I_{max}/I_{min}$  values and tibiae with higher TA and J values compared to all groups, likely due to increased loading patterns in one plane (Figures 3 and 4, and Table 4).

### Possible limitations

Due to the lack of archaeological attention in Baja California, Mexico, compared to other regions in North America, poor preservation in desert environments, and the burial practice of cremation, a dearth of archaeological materials was available for research in the Central Desert Sierras. While sample size is low for this region, due to these aforementioned variables, the skeletal remains used in this analysis are remarkable. Description of these materials is a necessary step to begin to elucidate the biological diversity of this important region in North American archaeology. Further projects in the Central Desert led by Baja Californian archaeologists will add valuable information to this report and aid in understanding the breadth of biological and cultural diversity in this hot-arid ecology.

## **Discussion**

The purpose of this paper was to describe body size, shape, and robusticity of two human populations in Holocene of Baja California, to illuminate the effects that heat, aridity, and maritime adaptations had on the biological and behavioral responses of Amerindians. We determined that individuals in the Cape Region were characterized by high body masses paired with tall statures, narrow bi-iliac breadths, and high intramembral indices, supporting some but not all of our predictions. Long-term isolation and adaptation to heat in this region is apparent in the narrow bi-iliac breadth and high intramembral indices indicating that despite limited variation in bi-iliac breadth of Early Holocene Amerindians, extreme heat may have resulted in eventual adaptation of this feature. The high body masses of these individuals were unexpected but may be

explained as a product of convenient access to freshwater springs in the Sierra de la Laguna and nearby coastal resources and relatively tall stature.

Results of our cross-sectional analyses support intense maritime adaptations indicating substantial support from oceanic resources that could have contributed to an increased body mass and stature. Humeri and lower limb robusticity values are most similar to, and even surpass, values in groups with intense activity in oceanic marine and terrestrial mountainous environments. These results support previous research that found high levels of femoral and tibial robusticity in non-industrialized individuals who inhabit rugged environments (Stock and Pfeiffer, 2004; Temple et al., 2021; Ruff, 1999; Marchi, 2008), and high levels of humeral robusticity in marine-hunter-gatherers who heavily rely on diverse oceanic resources (Stock and Pfeiffer, 2001; Stock, 2006; Temple et al., 2021; Weiss, 2003). Further, these results indicate that despite marine-hunter-gatherers having a localized food resource, similar to sedentary agricultural groups, high levels of mobility are required in desert ecologies potentially from the need to travel between freshwater springs and subsistence resources.

Sex-specific task specialization is also apparent in the upper and lower limbs of the Cape Region compared to other groups. Females in the Cape Region had decreased circularity in their right and left humeri but increased circularity in the femur compared to males. Males likely logically traversed from freshwater springs in Sierra de la Laguna to the coast for watercraft voyaging, whereas females locally procured shellfish and plant foods (Heizer and Massey, 1953; Baegert, 1979; Molto and Kennedy, 1991; Fujita, 2006). Humeral asymmetry is lower than predicted for males given archaeological and ethnohistoric accounts of the use of the atlatl but may support the notion that the atlatl

wasn't used during the Late Holocene (Massey, 1961). Conversely, high levels of bilateral humeral robusticity in males may reflect intense swimming behaviors given the presence of auditory exostoses in male crania and the importance of pearls and shellfish (Ainis et al., 2019; Leon-Portilla, 1970; del Barco, 1981; Shelvocke, 1992; Ainis et al., 2019; Gerhard, 1956). Together, body size, shape, and robusticity data support the notion that marine-hunter-gatherers in the Cape Region had abundant access to both freshwater and oceanic resources, resulting in long-term isolation, and a heat-adapted body type without signs of nutritional or aridity stress.

Human skeletal remains from the Central Desert Sierras differed in body size, shape, and robusticity that reflect both heat and resource scarcity adaptations, and decreased temporal or spatial isolation from nearby Amerindians. The high brachial indices and low body masses support biological responses to heat and aridity, while decreased statures may indicate increased nutritional stress. As the crural index is strongly influenced by population structure (Roseman and Auerbach, 2015), increased contact with northern Amerindian groups is plausible. Additionally, results of the cross-sectional analyses generally support decreased reliance on maritime adaptations indicating greater susceptibility to resource stress. Patterns of robusticity were generally higher in the lower limb, though due to low sample size did not reach significance. Humeri values are also remarkably low compared to other groups. High  $I_{max}/I_{min}$  values of the femur and humeri support increased loading patterns along one axis and aligns with research on semi-sedentary agriculturalists in mountainous environments who logistically forage and intensely procure foods using milling stations or mortar and pestles (Ruff and Hayes, 1983a; Bridges, 2005). Terrestrial foraging was favored over coastal foraging and

these results support these ethnohistoric and archaeological accounts for the Central Desert Sierras.

## Conclusion

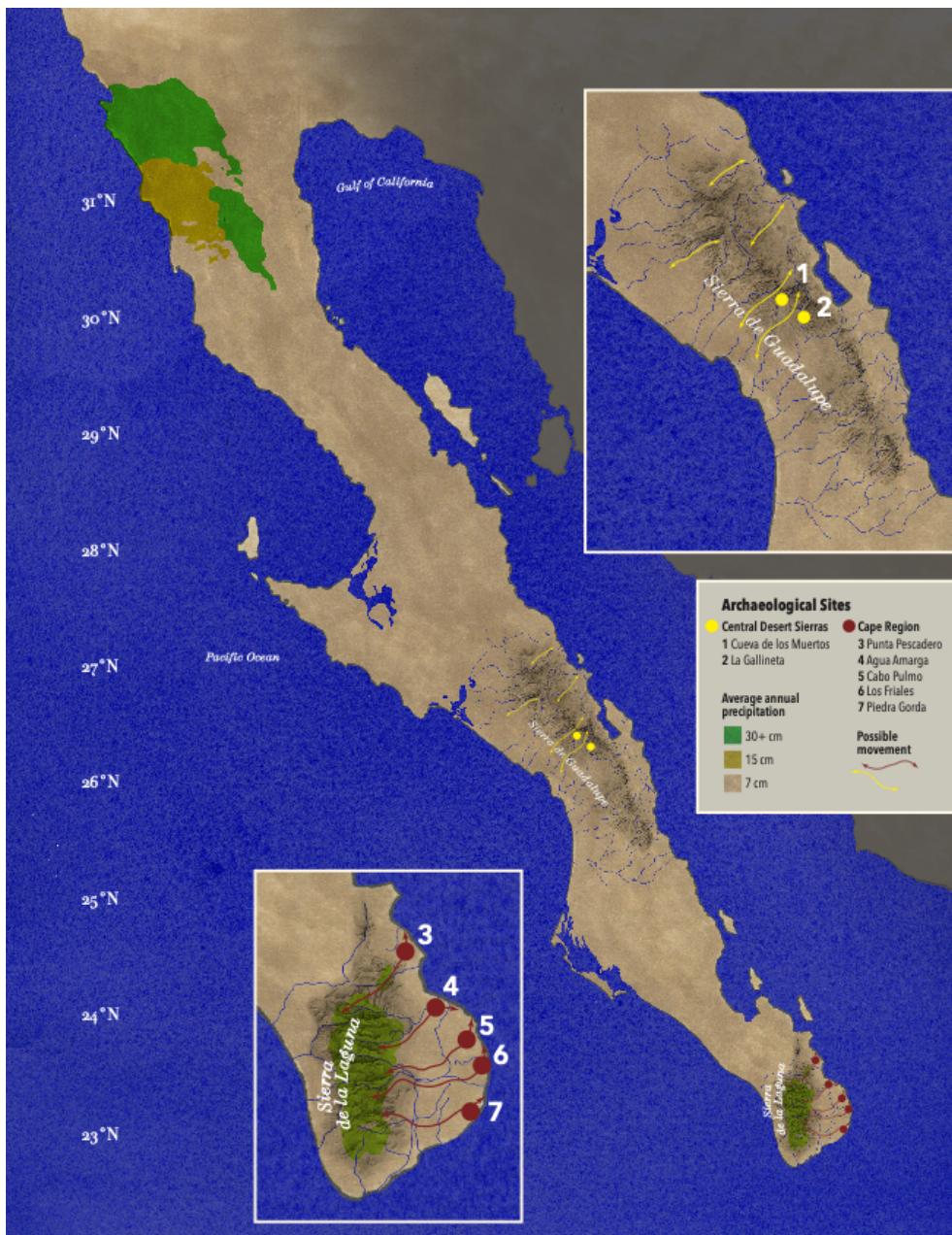
The Baja California peninsula thus supported diverse biological and behavioral dynamics of humans during the Holocene, despite intense heat and water constraints. While biological responses to heat and aridity are apparent for both the Cape Region (in bi-iliac breadth and intramembral proportions) and the Central Desert Sierras (in body mass and intramembral proportions), loading patterns associated with behavioral responses are markedly different for these two ecoregions. The human populations residing in the Cape Region likely experienced elevated spatial and temporal isolation, as well as greater access to environmental resources, including freshwater stocks (both from increased annual precipitation and associated groundwater), and marine fisheries. Together, these factors likely resulted in a heat-adapted body but a high body mass in this hot semi-arid region. Individuals in the Central Desert Sierras, who lived in an area that was less spatially convenient for access to both oceanic resources and freshwater springs, were possibly periodically affected by these biological constraints, resulting in lower stature and body mass. The dichotomy that humans are or aren't immune to insular evolutionary processes related to finite resources is likely too simplistic to explain the complex interactions that humans have with their local environments.

This collaborative research is setting new foundations for future research in the “Forgotten Peninsula” by tying diverse data on the cultural and biological complexity of these peoples with modern theory on human adaptation to extreme environments. As one

of the harshest ecologies in the world, Baja California holds important and extraordinary information about the peopling of North America, with Terminal Pleistocene occupation evident in northern and southern regions (Des Lauries et al., 2017; Fujita and Ainis, 2018; Sánchez and Flores, 2020). To interpret this information, a close collaboration and dialogue are required among anthropologists in Mexico and the United States to identify shared interests for informed interpretations of the past. This project is an attempt to bring together diverse voices by connecting this peninsula to larger discussions on North American prehistory. In doing so, we hope to have contributed to further understanding the incredible diversity of the past.

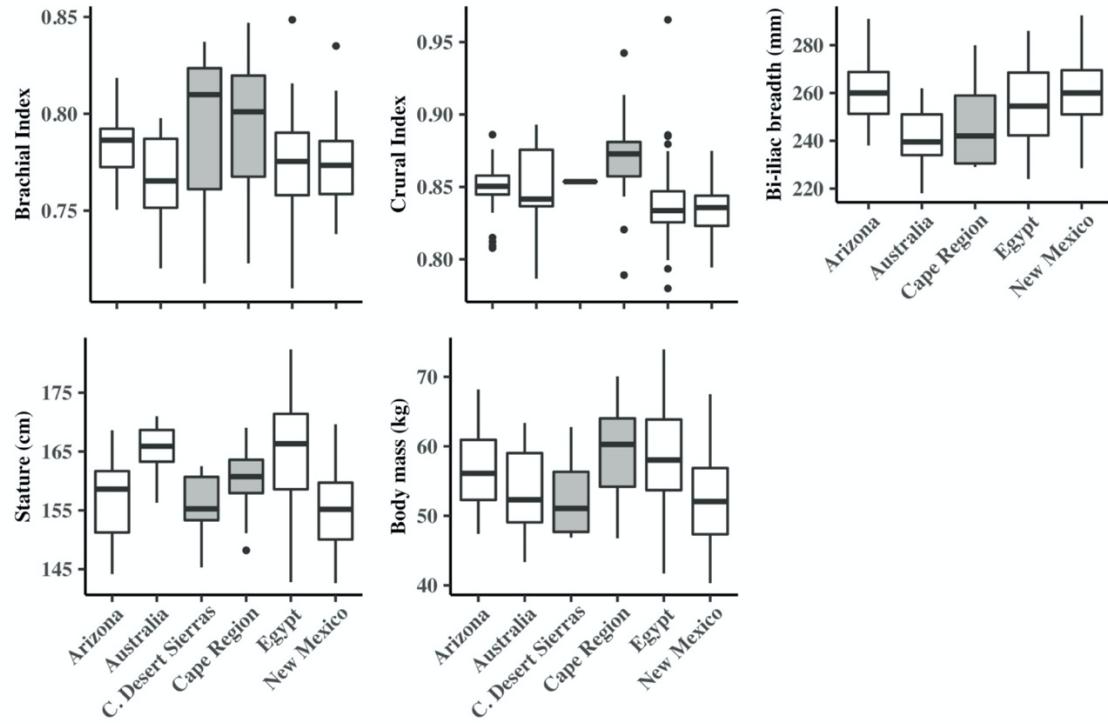
### **Acknowledgements**

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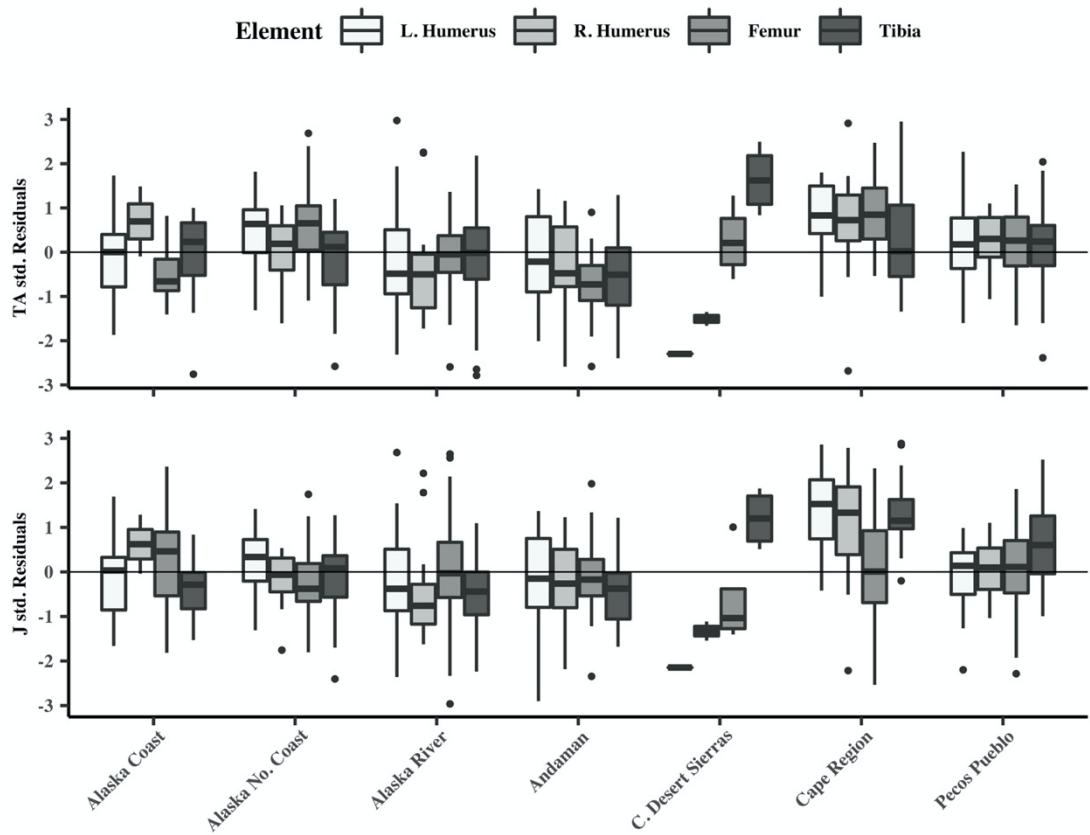


**Figure 4.1: Original map of Baja California with archaeological sites of the Central Desert Sierras and Cape Region used in analysis. Annual precipitation levels and freshwater springs are demarcated to highlight regional variation in aridity and resource dynamics. Individuals from the Central Desert, including the sierras, are purported to have moved in an east-west cline across the landscape, following these**

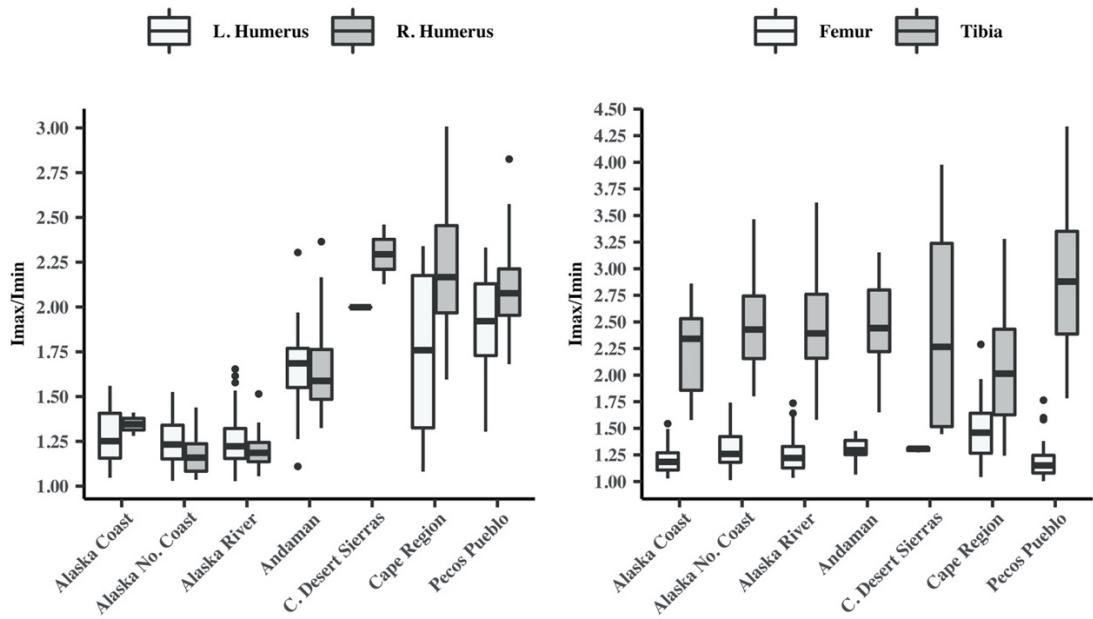
**springs, while the Cape Region moved to and from the coast and the Sierra de la Laguna. Illustration by Angele Mele.**



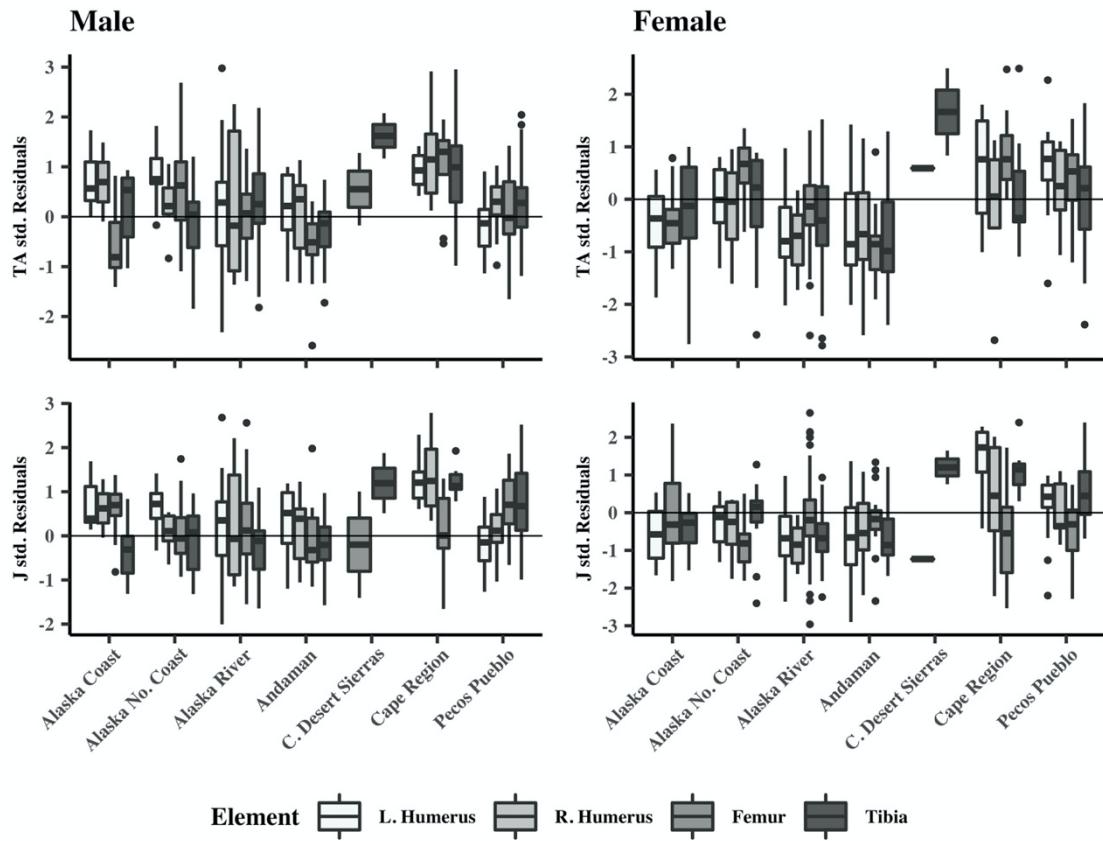
**Figure 4.2: Body size and proportions of Cape Region and Central Desert Sierras compared to similar latitudinal (23-26 – Egypt and Australia) and nearby Amerindians (New Mexico and Arizona). Grey highlight depicts Baja California Sur groups.**



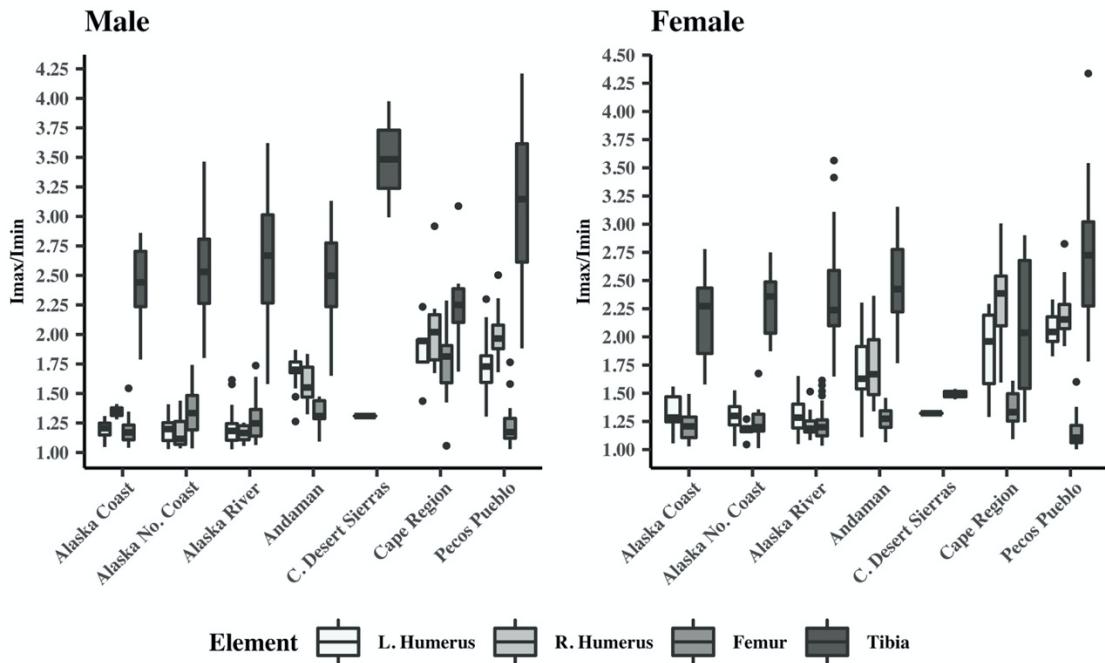
**Figure 4.3: Group comparisons of TA and J standardized residuals of left humerus, right humerus, femur, and tibia.**



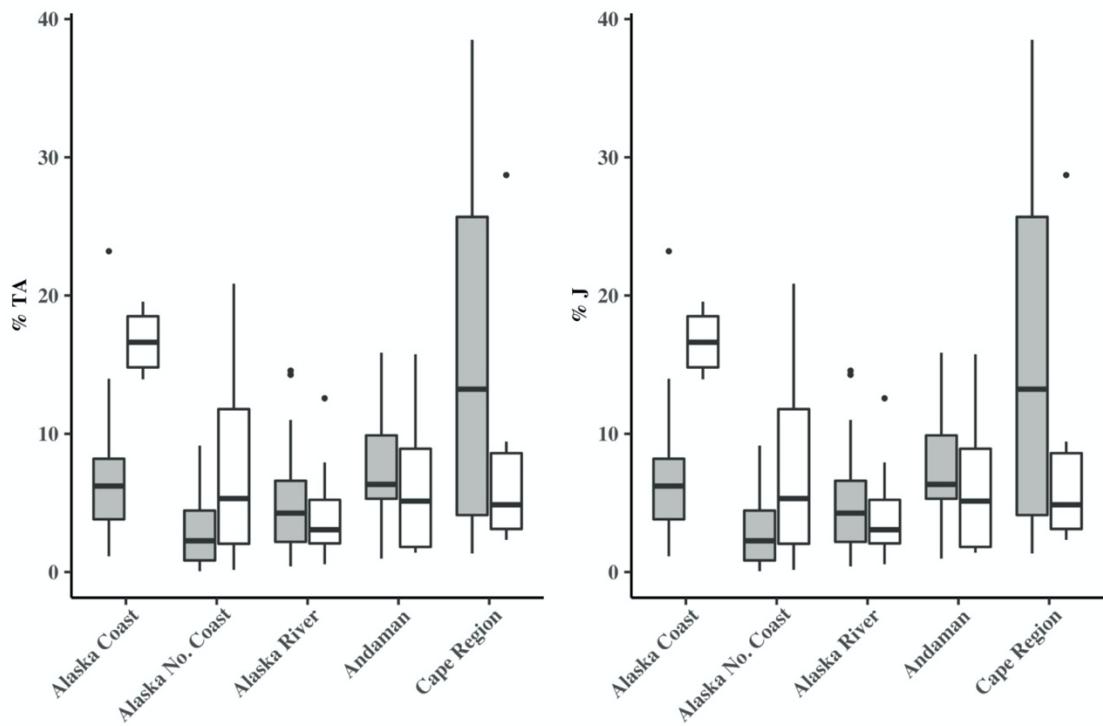
**Figure 4.4: Group comparisons of  $I_{\max}/I_{\min}$  shape ratios.**



**Figure 4.5: Box plots of sex-specific comparisons of J and TA standardized residuals.**



**Figure 4.6: Box plots of sex-specific comparisons of  $I_{\max}/I_{\min}$ .**



**Figure 4.7: Box plots of humeral bilateral asymmetry among groups; grey is female, white is male.**

**Table 4.1: Comparative samples used in study.**

Comparison	Sample	N	Time period	Subsistence	Note
Baja California	Cape Region	29	1320 - 1600 AD	Marine-hunter-gatherer	Semi-sedentary, heavy reliance on nearshore shellfish and pelagic fish and dolphins; latitude ~23 N (Fujita, 2006; Porcasi and Fujita, 2000; Ainis et al., 2019).
	Central Desert Sierras	6	BC 974 - 18 AD	Marine-hunter-gatherer	High levels of logistic mobility among water springs, and marine and terrestrial resources; latitude ~26 N (Baegert, 1952; Aschmann, 1967; Hyland and Gutiérrez, 2006).
Body size and proportions	Arizona	23	900 - 600 BP	Agriculture	Nearby Amerindian
	New Mexico	73	1000 - 300 BP	Agriculture	Nearby Amerindian
	Australia	15	<1000 BP?	Forager	Latitude ~ 25 S
	Egypt	81	4700 - 1550 BP	Agriculture	Latitude ~ 23 N
Cross-sectional geometry	Alaska Coast	25	1500 - 1800 CE	Marine-hunter-gatherer	Sedentary, intensive fish harvesting and marine mammal hunting, reduced mobility over rugged terrain (Temple et al., 2021).
	Alaska No. Coast	29	600 - 1500 CE	Marine-hunter-gatherer	Semi-sedentary, intensive hunting, seasonal mobility, rugged terrain (Temple et al., 2021).
	Alaska River	79	300 - present	Hunter-gatherer	High levels of logistic mobility from mountainous to riverine areas (Temple et al., 2021).
	Andaman Island	25	Protohistoric	Marine-hunter-gatherer	High levels of swimming and benthic and pelagic marine foraging (Stock and Pfieffer, 2001).
	Pecos Pueblo	29	1300 - 1828 AD	Agriculture	Sedentary with logistical hunting and foraging in mountainous terrain (Ruff and Hayes, 1983a).

**Table 4.2: Mann-Whitney pairwise u test with Holm-Bonferroni correction among groups in the Baja California peninsula, nearby Amerindians, and similar latitude.**

Location	Statistic	Cape Region					Central Desert Sierras				
		n=28	n=28	n=19	n=20	n=25	n=6	n=4	n=3	n=4	
		Stature (cm) <sup>†</sup>	BM (kg) <sup>‡</sup>	BIB (mm)	Brachial	Crural	Stature (cm)	BM (kg)	Brachial	Crural	
Nearby Amerindians	Mean	157.016	56.838	261.283	0.784	0.847	(n=23)	0.747	0.303	0.505	0.870
	(sd)	(7.130)	(6.482)	(13.814)	(0.019)	(0.021)					
	p-value	0.083	0.263	0.017**	0.238	0.008**					
New Mexico	Mean	155.523	52.408	259.664	0.773	0.834	(n=73)	0.878	0.918	0.367	0.351
	(sd)	(6.586)	(6.118)	(13.763)	(0.020)	(0.019)					
	p-value	0.001**	0.000**	0.007**	0.007*	0.000**					
Latitude 23-26	Mean	165.827	53.640	241.167	0.765	0.848	(n=15)	0.003**	0.961	0.427	0.875
	(sd)	(7.130)	(6.245)	(11.712)	(0.026)	(0.032)					
	p-value	0.010**	0.021*	0.953	0.013*	0.008**					
Egypt	Mean	164.633	58.101	255.019	0.774	0.838	(n=81)	0.021*	0.133	0.367	0.375
	(sd)	(9.780)	(7.030)	(15.880)	(0.240)	(0.024)					
	p-value	0.012*	0.601	0.099	0.016*	0.000**					

\*significant (p-value < 0.05)

\*\*significant with multiple comparison corrections

**Table 4.3: Results of Mann-Whitney pair-wise comparisons of left humeral properties.**

		Cape Region		Central Desert Sierras	
		Left Humerus	Right Humerus	Left Humerus	Right Humerus
		n=17	n=16	n=1	n=2
<b>Alaska Coast</b>	TA	0.004*	1.000	0.077	0.333
	J	0.000**	0.549	0.077	0.333
	$I_{\max}/I_{\min}$	0.038*	1.000	0.231	1.000
	n	25	2		
<b>Alaska No. Coast</b>	TA	0.181	0.050	0.067	0.051
	J	0.001**	0.004*	0.067	0.103
	$I_{\max}/I_{\min}$	0.012*	0.072	0.467	0.555
	n	29	11		
<b>Alaska River</b>	TA	0.000**	0.003**	0.050*	0.104
	J	0.000**	0.000**	0.050*	0.173
	$I_{\max}/I_{\min}$	0.010*	0.080	0.275	0.573
	n	79	20		
<b>Andaman</b>	TA	0.003*	0.003*	0.080	0.036*
	J	0.000**	0.000**	0.154	0.050*
	$I_{\max}/I_{\min}$	0.689	0.380	0.074	0.011*
	n	25	30		
<b>Pecos Pueblo</b>	TA	0.023*	0.035*	0.067	0.004*
	J	0.000**	0.001**	0.133	0.004*
	$I_{\max}/I_{\min}$	0.069	0.041*	0.067	0.003**
	n	29	31		
<b>Central Desert Sierras</b>	TA	0.111	0.052	-	-
	J	0.111	0.052	-	-
	$I_{\max}/I_{\min}$	1.000	0.521		
	n	1	2		

\*significant (p-value < 0.05)

\*\*significant with multiple comparison corrections

**Table 4.4: Results of Mann-Whitney pair-wise comparisons of lower limb properties.**

		Cape Region		Central Desert Sierras	
		Femur	Tibia	Femur	Tibia
		n=25	n=22	n=4	n=4
<b>Alaska Coast</b>	TA	0.000**	0.000**	0.073	0.001**
	J	0.671	0.702	0.213	0.001**
	$I_{\max}/I_{\min}$	0.000*	0.216	0.120	1.000
	n	31	28.000		
<b>Alaska No. Coast</b>	TA	0.281	0.000**	0.450	0.005**
	J	0.358	0.579	0.269	0.001**
	$I_{\max}/I_{\min}$	0.014*	0.018*	0.803	0.894
	n	32	29.000		
<b>Alaska River</b>	TA	0.000**	0.000**	0.450	0.000**
	J	0.842	0.470	0.164	0.000*
	$I_{\max}/I_{\min}$	0.000**	0.006*	0.222	0.777
	n	105	95.000		
<b>Andaman</b>	TA	0.000**	0.000**	0.032*	0.001**
	J	0.523	0.044*	0.160	0.000**
	$I_{\max}/I_{\min}$	0.015*	0.012*	0.955	0.852
	n	31	29.000		
<b>Pecos Pueblo</b>	TA	0.003**	0.004**	0.947	0.145
	J	0.807	0.687	0.176	0.003*
	$I_{\max}/I_{\min}$	0.000**	0.000**	0.057	0.429
	n	60	59		
<b>Central Desert Sierras</b>	TA	0.216	0.725	-	-
	J	0.341	0.045*	-	-
	$I_{\max}/I_{\min}$	0.445	0.803		

\*significant (p-value < 0.05)

\*\*significant with multiple comparison corrections

**Table 4.5: Results of Mann-Whitney sex-specific pair-wise comparisons of TA and J.**

		Cape Region							
		Left Humerus		Right Humerus		Femur		Tibia	
		Male = 5	Female = 6	Male = 7	Female = 6	Male = 9	Female = 7	Male = 6	Female = 7
<b>Alaska Coast</b>	TA	0.435 0.001*	0.062 0.001*	1.000	-	**	0.014*	**	0.000*
	J	0.093	*	0.500	-	0.193	0.001*	0.35	0.901
	$I_{\max}/I_{mi}$	0.002*	*	0.056	-	0.002	0.025*	0.462	0.757
	n	8	17	2	0	12	19	11	17
<b>Alaska No. Coast</b>	TA	0.94	0.151	0.950	0.792	0.253	1	**	0.004
	J	0.071	0.005*	0.014	0.537	0.764	1	0.077	0.93
	$I_{\max}/I_{mi}$	0.003*	0.001	0.004*	0.004				
	n	0.000**	*	**	*	**	0.083	0.31	0.5536
	n	17	12	6	5	20	12	18	11
<b>Alaska River</b>	TA	0.026*	0.012*	1.000	0.239	**	0.019*	**	*
	J	0.016*	*	0.138	0.109	0.849	0.002*	0.287	0.387
	$I_{\max}/I_{mi}$	0.000*	0.001	0.000*	0.000				
	n	0.000**	*	**	*	**	0.012*	0.179	0.327
	n	18	41	6	14	46	57	43	52
<b>Andaman</b>	TA	0.046*	0.031*	0.350	0.302	**	0.003*	**	0.000*
	J	0.046*	*	*	0.154	0.487	0.000*	*	0.045
	$I_{\max}/I_{mi}$	0.003*	0.016	0.001	0.014*	0.003			
	n	0.046*	*	*	*	**	0.012*	0.179	0.327
	n	0.117	0.263	**	*	**	0.162	0.424	0.197
	n	13	10	14	15	16	15	15	14
						0.010			
<b>Pecos Pueblo</b>	TA	0.002** 0.004	0.968	0.320	0.641	*	1	0.235	0.054
	J	0.001**	0.012*	*	0.59	0.08	0.37	0.48	0.776
	$I_{\max}/I_{mi}$	0.395	0.547	0.945	0.494	0.002	0.006	*	0.032*
	n	15	14	15	16	30	30	29	30

\*significant (p-value < 0.05)

\*\*significant with multiple comparison corrections

**Table 4.6: Results of Mann-Whitney pair-wise with Holm-Bonferroni correction comparisons of Humeral Asymmetry.**

	Cape Region					
	Combined = 13		Male = 6		Female = 4	
	TA	J	TA	J	TA	J
Alaska Coast (n=14)	0.830	0.326	0.114	0.114	0.635	0.839
Alaska No. Coast (n=23)	0.123	0.253	0.910	0.791	0.109	0.109
Alaska River (n=61)	0.046*	0.126	0.135	0.233	0.233	0.326
Andaman Island (n=29)	0.519	0.790	0.701	1.000	0.753	0.753

## Literature cited

- Allen JA. 1887. The influence of physical conditions on the genesis of species. *Rad Rev* 1:108-140.
- Aschmann Homer. 1952 A fluted point from central Baja California. *Am Antiq* 17:262-263.
- Aschmann Homer. 1967. The Central Desert of Baja California: demography and ecology. Manessier Publishing Company, Riverside.
- Auerbach B. 2012. Skeletal variation among early Holocene North American humans: implications for origins and diversity in the Americas. *Am J Phys Anth* 169:525-536.
- Auerbach BM, Ruff CB. 2004. Human body mass estimation: a comparison of “morphometric and “mechanical” methods. *Am J Phys Anth* 125:331-342.
- Auerbach BM, Ruff CB. 2010. Stature estimation formulae for Indigenous North American populations. *Am J Phys Anth* 141:190-207.
- Baegert, Johann Jakob. 1952. Observations in Lower California. Edited by M.M. Brandenburg and Carl L. Baumann. University of California Press, Berkeley.
- Baegert Johan Jakob. 1979. Observations in Lower California. Edited by M.M. Brandenburg and Carl L. Baumann. University of California Press, Berkeley.
- Bergmann C. 1847. Ueber die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3:595-708.
- Barron JA, Metcalfe SE, Addison JA. 2012. Response of the North American monsoon to regional changes in ocean surface temperature. *Paleooceanogr* 27:PA3206.
- Belding L. 1885. The Pericue Indians. *West-Am Sci* 1:21-22.

Berger B. 1998. Almost an Island: travels in Baja California. University of Arizona Press, Tucson.

Bethancourt HJ, Swanson ZS, Nzunza R, Huanca T, Conde E, Larry KW, Young SL, Ndiema E, Braun D, Pontzer H, Rosinger AY. 2020. Hydration in relation to water insecurity, heat index, and lactation status in two small-scale populations in hot-humid and hot-arid environments. *Am J Hum Biol* 33:1-25.

Braje TJ, Erlandson JM, Timbrook J. 2005. An asphaltum coiled basket impression, tarring pebbles, and Middle Holocene water bottles from San Miguel Island, California. *J Calif Great Bas Arch* 25:207-213.

Bridges PS. 1989. Changes in activities with the shift to agriculture in the Southeastern United States. *Curr Anthropol* 30:385-394.

Bridges PS. 2005. Skeletal biology and behavior in ancient humans. *Evol Anthropol* 4:112-120.

Bridges PS, Blitz JH, Solano MC. 2000. Changes in long bone diaphyseal strength with horticultural intensification in west-Central Illinois. *Am J Phys Anth* 112:217-238.

Brooks N. 2006. Cultural responses to aridity in the Middle Holocene and increased social complexity. *Quatern Int* 151:29-49.

Brooks S, Suchey JM. 1990. Skeletal age determination based on the os pubis: a comparison of the Acsádi-Nemeskéri and Suchey-Brooks methods. *J Hum Evo* 5:227-238.

Buikstra J, Ubelaker D. 1994. Standards for data collection of human skeletal remains. Report Number 44. Fayetteville, AR: Arkansas Archaeological Survey.

Cariño, M. 2021. Oasidad: patrimonio biocultural in Equilibrio: Custodios de la Sierra. Beta Diversidad A.C., Febrero 2021.

Clavijero FJ. 1937. The history of (lower) California. Edited by Gray AA. Stanford University Press, Stanford, California.

Cowgill LW, Eleazer CD, Auerbach BM, Temple DH, Okazaki K. 2012. Developmental variation in ecogeographic body proportions. *Am J Phys Anth* 148:557-570.

Cremaschi M, Di Lernia S. 1999. Holocene climatic changes and cultural dynamics in the Libyan Sahara. *Afr Arch Rev* 16:211-238.

Crutzen PJ. 2006. The Anthropocene. *Earth System Science in the Anthropocene*. Springer, Berlin: Heidelberg 13-18.

de Alba R. 2021. La Giganta y Guadalupe: guardianas de la vida en la Península in Equilibrio: Custodios de la Sierra. Beta Diversidad A.C., Febrero 2021.

de la Ascensión A. 1602. Father Antonio de la Ascensión's account of the voyage of Sebastian Vizcaino: 1602. 1929, translated by Wagner HR in Ethnology of the Baja California Indians, Mathes M ed, 164-208. Spanish Borderland Sourcebooks 5. Garland Publishing, New York.

de Salvatierra JM. 1971. Selected letters about lower California. Translate and annotated by Ernest J. Burrus, S.J. Dawson's Book Shop, Los Angeles.

del Angel A, Cisneros HB. 2004. Technical note: modification and regression equations used to estimate stature in Mesoamerican skeletal remains. *Am J Phys Anth* 125:264-265.

del Barco M. 1973. Historia natural y crónica de la antigua California. Edited by Miguel León-Portilla. Universidad Nacional Autónoma de México, Mexico City.

del Barco M. 1980. The natural history of Baja California. Dawson's Book Shop, Los Angeles.

del Barco M. 1981. Ethnology and linguistics of Baja California. Dawson's Book Shop, Los Angeles.

- deMonocal PB. 2001. Cultural responses to climate change during the Late Holocene. *Science* 292:1-7.
- Demes B. 2007. In vivo bone strain and bone functional adaptation. *Am J Phys Anth* 133: 717-722.
- Des Lauries MR. 2010. Island of fogs: archaeological and ethnohistorical investigations of Isla Cedros, Baja California. Salt Lake City, UT: University of Utah Press.
- Des Lauries MR, Davis LG, Turnbull III J, Southon JR, Taylor RE. 2017. The earliest shell fishhooks from the Americas reveal fishing technology of Pleistocene maritime foragers. *Am Antiq* 82:498.
- Diaz SC, Touchan R, Swetnam TW. 2001. A tree-ring reconstruction of past precipitation for Baja California Sur, Mexico. *Int J Climat* 21, 1007-1019.
- Dobzhansky T. 1963. Biological evolution in island populations, in Man's place in the island ecosystem. Edited by Fosberg F, 65-74. Honolulu: Bishop Museum Press.
- Dozier EP. 1970. The Pueblo Indians of North America. Waveland Press Inc. Long Grove, Illinois.
- Diguet L. 1905. Anciennes sépultures Indigénes de la Basse-Californie Méridionale. *J Soc Américanistes Paris* 2:329-333.
- Erlandson JM, Fitzpatrick SM. 2006. Oceans, islands, and coasts: current perspectives on the role of the sea in human prehistory. *J Isla Coast Arch* 1:5-32.
- Eveleth PB, Tanner JM. 1976. Worldwide variation in human growth. 8. CUP Archive.
- Fujita H. 2006. The Cape Region. In *The Prehistory of Baja California: Advances in the Archaeology of the Forgotten Peninsula*, edited by Laylander D and Moore JD, 82-98. University of Florida Press, Gainesville.
- Fujita H, Ainis AF. 2018. Traditions of early human groups in Baja California and possible routes for the peopling of the peninsula. *West Nor Am Nat* 78:285-301.

Fujita H, Minagawa M. 2004. High consumption of marine resources and CAM plants among prehistoric humans of southern Baja California inferred from carbon and nitrogen isotope analysis. Paper presented in the 38<sup>th</sup> Annual Meeting of the Society for California Archaeology, Riverside.

Genoves S. 1967. Proportionality of the long bones and their relation to stature among Mesoamericans. *Am J Phys Anth* 26:67-78.

Gosling SN, Arnell, NW. 2016. A global assessment of the impact of climate change on water scarcity. *Climate Change* 134:371-385.

Grine FE, Jungers WL, Tobias PV, Pearson OM. 1995. Fossil *Homo* femur from Berg Aukas, northern Namibia. *Am J Phys Anth* 26:67-78.

Guillén, Clemente. 1979. Explorer of the south: diaries of the Overland Expeditions to Bahia Magdalena and La Paz, 1719, 1720-1721. Translated and edited by W. Michael Mathes. Dawson's Book Shop, Los Angeles.

Gutiérrez Martínez ML. 2003. El estilo Gran Mural en la Sierra de Guadalupe, B.C.S. *Arqueol Mexi* 11:41-45.

Gutiérrez Martínez ML. 2019. Between mountains, plains, and sea: prehistoric cultural adaptations and climatic regions in the Sierras de San Francisco and Guadalupe, Baja California Sur. *Pac Coast Arch Quart* 54:116-154.

Gutiérrez Martínez ML. personal communication. February 2021. Radiocarbon dates of skeletal remains from Cueva de los Muertos and La Gallineta archaeological sites in the Baja California Central Desert complex.

Haapasalo H, Kontulainen S, Sievanen H, Kannus P, Jarvinen M, Vuori I. 2000. Exercise-induced bone gain is due to enlargement in bone size without a change in volumetric bone density: a peripheral quantitative computed tomography study of the upper arms of male tennis players. *Bone* 27:351-357.

- Hastings JR, Turner RM. 1965. Precipitation regimes in Baja California, Mexico. *Geografiska Annaler: Series A, Physical Geography* 47:204–23.
- Heizer RF, Massey WC. 1953. Aboriginal navigation off the coasts of Upper and Baja California. 151. US Government Printing Office.
- Henrickson CN. 2013. The Archaeology of Cueva Santa Rita: A Late Holocene Rockshelter in the Sierra de La Giganta of Baja California Sur, Mexico. University of California, Berkeley.
- Holliday TW. 1997. Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evo* 32:423-447.
- Holliday TW. 1999. Brachial and crural indices of European Late Upper Paleolithic and Mesolithic humans. *J Hum Evo* 36:549-566.
- Holliday TW. 2002. Body size and postcranial robusticity of European Upper Paleolithic hominins. *J Hum Evo* 43:513-528.
- Hora M, Pontzer H, Wall-Scheffler CM, Sládek V. 2020. Dehydration and persistence hunting in *Homo erectus*. *J Hum Evo* 138:102682.
- Houghton P. 2009. People of the great ocean: aspects of human biology of the early Pacific. Cambridge University Press.
- Hyland J. 2006. The Central Sierras in The prehistory of Baja California: advances in the archaeology of the forgotten peninsula edited by Laylander D, Moore JD. University Press of Florida, Gainesville.
- Hyland J, Gutiérrez ML. 1995. An obsidian fluted point from Central Baja California. *J Great Bas Arch* 17:126-128.
- Jones HH, Priest JD, Hayes WC, Tichenor CC, Nagel DA. 1977. Humeral hypertrophy in response to exercise. *J Bone Joint Surg.* 59:204-208.

- Kaneshiro KY. 1995. Evolution, speciation, and genetic structure of island populations. In Ecological Studies, 115. Ed, Vitousek et al. Springer-Verlag Berlin Heidelberg.
- Kasabova BE, Holliday TW. 2015. New model for estimating the relationship between surface area and volume in the human body using skeletal remains. Am J Phys Anth 156:614-624.
- Katzmarzyk P, Leonard WR. 1998. Climatic influences on human body size and proportions: ecological adaptations and secular trends. Am J Phys Anth 106:483-503.
- Keegan WF, Diamond JM. 1987. Colonization of islands by humans: a biogeographical perspective. Ad Arch Meth Theor 10:49-92.
- King JH. 1997. Prehistoric diet in Central Baja California, Mexico. Thesis: Master of Arts in the Department of Anthropology. Simon Fraser University.
- Kirch PV. 1980. Polynesian prehistory: cultural adaptation in island ecosystems. Am Sci 68:39-48.
- Kirch PV. 1986. Exchange systems and inter-island contact in the transformation of an island society: the Tikopia case, in Island societies: archaeological approaches to evolution and transformation. Edited by Kirch PV, 33-21. Cambridge: Cambridge University Press.
- Kirch PV, Green RC. 1987. History, phylogeny, and evolution in Polynesia. Curr Anthr 28:431-456.
- Kirch PV, Hunt TL. 1997. Historical ecology in the Pacific Islands: prehistoric environmental and landscape change. Yale University Press.
- Krutch JW. 1961. The forgotten peninsula: a naturalist in Baja California. William Sloan Associates, New York.

- Kuzawa CW, Bragg JM. Plasticity in human life history strategy: implications for contemporary human variation and the evolution of the genus *Homo*. *Curr Anthr* 53:S369-S382.
- Lane CS, Horn SP, Kerr MT. 2014. Beyond the Mayan Lowlands: impacts of the Terminal Classic Drought in the Caribbean Antilles. *Quatern Sci Rev* 86:89-98.
- Laylander DP. 1987. Sources and strategies for the prehistory of Baja California. Master's thesis, Department of Anthropology, San Diego State University, San Diego.
- Laylander DP, Moore JD. 2006. *The Prehistory of Baja California: Advances in the Archaeology of the Forgotten Peninsula*. Gainesville: University of Florida Press.
- Leach WN. unpublished 2006. Alaskan eskimo and Polynesian Island population skeletal anatomy: the “pacific paradox” revisited through surface area to body mass comparisons. Thesis: Master of Arts in Anthropology, The University of Montana, Missoula, MT.
- León-Portilla M. 1970. Testimonios sudcalifornianos: nueva entrada y establecimiento en el Puerto de la Paz, 1720. Instituto de Investigaciones Históricas, serie documental no. 9. Mexico City: Universidad Nacional Autónoma de México.
- Lovejoy CO. 1985. Dental wear in the Libben population: its functional pattern and role in determination of adult skeletal age at death. *Am J Phys Anth* 68:47-56.
- Lovejoy CO, Meindl RS, Pryzbeck TR, Mensforth RP. 1985. Chronological metamorphosis of the auricular surface of the ilium: a new method for determination of adult skeletal age at death. *Am J Phys Anth* 68:15-28.
- Macfarlan SJ, Henrickson CN. 2010. Inferring relationships between indigenous Baja California Sur and Seri/Comcáac populations through cultural traits. *J Cali Great Bas Arch* 30:51-68.

- Macfarlan SJ, Schacht R, Foley C, Cahoon S, Osusky G, Vernon KB, Tayler E, Henrickson C, Schniter E. 2020. Marriage dynamics in old Lower California: ecological constraints and reproductive value in an arid peninsular frontier. *Biodemo Soc Biol* 65:156-171.
- Macintosh AA, Davies TG, Ryan TM, Shaw CN, Stock JT. 2013. Periosteal versus true cross-sectional geometry: a comparison along humeral, femoral, and tibial diaphyses. *Am J Phys Anth* 150:442-452.
- Marchi D. 2008. Relationships between lower limb cross-sectional geometry and mobility: the case of a Neolithic sample from Italy. *Am J Phys Anth* 137:188-200.
- Massey W. 1947. Brief report on archaeological investigations in Baja California. *Southwest J Anthr* 3:344-359.
- Massey W. 1949. Tribes and languages of Baja California. *Southwest J Anthr* 5:272-307.
- Massey W. 1955. Culture history in the Cape Region of Baja California, Mexico. Ph.D. dissertation, University of California, Berkeley.
- Massey W. 1961. The survival of the dart-thrower on the peninsula of Baja California. *Southwest J Anthr* 17:81-93.
- Massey W. 1966. Archaeology and Ethnohistory of Lower California. In *Handbook of Middle American Indians*, Volume 4, edited by Ekholm GF and Willey GR, 38-58. University of Texas Press, Austin.
- Massey WC and Osborne CM. 1961. A burial cave in Baja California: the Palmer Collection, 1867. *UC Anthr Rec* 16:336-363.
- Mathes WM. 1975. Some new observations relative to the Indigenous inhabitants of La Paz, Baja California Sur. *J Cali Anthr* 2:180-182.
- Mathes WM. 1989. Baja California: a special area of contact and colonization, 1535-1697. In *Columbian consequences*, Vol 1: Archaeological and historical

perspectives on the Spanish Borderlands West, Thomas DH (ed.) 407-422.  
Smithsonian Institution, Washington, D.C.

Mathes WM. 2006. Ethnohistoric evidence. In The Prehistory of Baja California: advances in the archaeology of the forgotten peninsula, ed Laylander D and Moore JD, 42-66. University of Florida Press, Gainesville.

Maya C, Coria R, Dominguez R. 1997. Caracterizacion de los Oasis. In Arriaga L. Rodriquez-Estrella R., editors. Los Oadsis de la Peninsula de Baja California, Mexico. La Paz, BCS, Mexico: CIBNOR, 5-26.

McHenry HM. 1992. Body size and proportions in early Hominids. Am J Phys Anth 30:297-301.

Meindl RS and Lovejoy CO. 1985. Ectocranial suture closure: a revised method for the determination of skeletal age at death based on the lateral-anterior sutures. Am J Phys Anth 68:79-85.

Mixco MJ. 1977. JP Harrington's Cochimi Vocabularies. J Cali Anthr 4:42-49

Mixco MJ. 2006. The Indigenous languages in The prehistory of Baja California: advances in the archaeology of the forgotten peninsula ed Laylander D and Moore JD. University Press of Florida, Gainesville.

Molto JE. 2015. Malintent trauma among prehistoric Las Palmas people. Pacific Coast Archaeological Society Quarterly 51, 61-78.

Molto JE, Fujita H. 1995. La Matancita: A Las Palmas Mortuary Site from the West Cape Region of Baja California Sur, Mexico. Pacific Coast Archaeological Society Quarterly, 31, 20-55.

Molto JE, Kennedy B. 1991. Diet of the Las Palmas culture of the Cape Region, Baja California Sur. Pac Coast Arch Soc Quart 27:47-59.

Napolí IM. 1721. The Cora Indians of Baja California. 1970, Translated by Moriarty III JR and Smith BF. Dawson's Book Shop, Los Angeles.

North AW. 1908. The native tribes of lower California. Am Anthr 10:236-250.

O'Neill MC, Ruff CB. 2004. Estimating human long bone cross-sectional geometric properties: a comparison of noninvasive methods. J Hum Evo 47:221-235.

Pearson OM, Lieberman DE. 2004. The aging of Wolff's "law": ontogeny and responses to mechanical loading in cortical bone. Am J Phys Anth S39:63-99.

Pietruszewsky M. 1970. An osteological view of indigenous populations in Oceania. Pac Anthr Rec 11:1-12.

Pontzer H, Brown MH, Wood BH, Raichlen DA, Mabulla AZP, Harris JA, Dunsworth H, Hare B, Walker K, Luke A, Dugas LR, Schoeller D, Plange-Rhule J, Bovet P, Forrester TE, Thompson ME. 2021. Evolution of water conservation in humans. Curr Biol 31:1-7.

Raghavan M, et al. 2015. Genomic evidence for the Pleistocene and recent population history of Native Americans. Science 349:6250.

Ritter E. 1979. An archaeological study of South-Central Baja California, Mexico, Ph.D. dissertation, University of California, Davis.

Ritter E. 2006. South-Central Baja California in The prehistory of Baja California: advances in the archaeology of the forgotten peninsula ed, Laylander D and Moore JD. University Press of Florida, Gainesville.

Rivet P. 1909 Recherches Anthropologiques sur la Basse-California. J Soc Américan 6:147–253.

Roseman C, Auerbach B. 2015. Ecogeography, genetics, and the evolution of human body form. J Hum Evo 78:80-90.

- Ruff C. 1987. Sexual dimorphism in human lower limb bone structure: relationship to subsistence strategy and sexual division of labor. *J Hum Evo* 16:391-416.
- Ruff C. 1994. Morphological adaptation to climate in modern and fossil hominids. *Year Phys Anthr* 37:65-107.
- Ruff C. 2019. Biomechanical analyses of archaeological human skeletons. In Katzenberg MA & Saunders SR Eds., *Biological anthropology of the human skeleton* 2:189–224. Hoboken: Wiley Blackwell.
- Ruff C. 2002. Variation in human body size and shape. *Ann Rev Anthropol* 31:211-232.
- Ruff C, Larsen CS, Hayes WC. 1984. Structural changes in the femur with the transition to agriculture on the Georgia coast. *Am J Phys Anth* 64:125-136.
- Ruff C, Hayes W. 1983a. Cross-sectional geometry of Pecos Pueblo femora and tibiae—a biomechanical investigation: I. Method and general patterns of variation. *Am J Phys Anth* 60:359-381.
- Ruff C, Hayes W. 1983b. Cross-sectional geometry of Pecos Pueblo femora and tibiae—a biomechanical investigation: II. Sex, age, and side differences. *Am J Phys Anth* 60:383-400.
- Ruff C, Scott WW, Liu A Y-C. 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am J Phys Anth* 86:397-413.
- Ruff C, Holt B, Trinkaus E. 2006. Who's afraid of the big bad Wolff?: “Wolff’s law” and bone functional adaptation. *Am J Phys Anth* 129:484-498.
- Ruff CB, Trinkaus E, Walker A, Larsen CS. 1993. Postcranial robusticity in Homo. I: temporal trends and mechanical interpretation. *Am J Phys Anthropology* 91:21-53.

Sales L. 1956. Observations on California 1772—1790, translated and edited by Rudkin CN. Dawson's Book Store, Los Angeles.

Salinas Zavala CA, Leyva Contreras D, Lluch B, Rivera ED. 1990. Distribución geográfica y variabilidad climática de los regimens pluviomeétricos en Baja California Sur, México. *Atmosfera* 3:217–37.

Sánchez AR. 2013. Tendiendo redes. Fondo Nacional para la Cultura y las Artes, La Paz, Baja California Sur, Mexico.

Santoro CM et al., 2016. Continuities and discontinuities in the socio-environmental systems of the Atacama Desert during the last 13,000 years. *J Anthr Arch* 46:28-39.

Schewe J, et al. 2014. Multimodel assessment of water scarcity under climate change. *PNAS* 9:3254-3250.

Shaw CN, Stock JT. 2009. Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *Am J Phys Anth* 140:160-172.

Shelvocke G. 1992. [1726] Cabo San Lucas: August 1721. In Ethnology of the Baja California Indians, Mathes M (ed) 306-333. Spanish Borderland Sourcebooks 5. New York: Garland Publishing.

Sparacello VS, Pearson OM. 2010. The importance of accounting for the area of the medullary cavity in cross-sectional geometry: a test based on the femoral midshaft. *Am J Phys Anth* 143:612-624.

Stock JT, Pfeiffer SK. 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman Islands. *Am J Phys Anth* 115:337-348.

- Stock JT, Pfeiffer SK. 2004. Long bone robusticity and subsistence behaviour among Later Stone Age foragers of the forest and fynbos biomes of South Africa. *J Arch Sci* 31:999-1013.
- Stock JT, Shaw CN. 2007. Which measures of diaphyseal robusticity are robust? A comparison of external methods of quantifying the strength of long bone diaphyses to cross-sectional geometric properties. *Am J Phys Anth* 134:412-423.
- Temple DH, Matsumura H. 2011. Do body proportions among Jomon foragers from Hokkaido conform to ecogeographic expectations? Evolutionary implications of body size and shape among northerly hunter-gatherers. *Int J Osteoarch* 21:268-282.
- Temple DH, Rosa ER, Hunt DR, Ruff CB. 2021. Adapting in the Arctic: habitual activity and landscape interaction in Late Holocene hunter-gatherers from Alaska. *Am J Phys Anth* DOI: 10.1002/ajpa.24250
- Templeton AR. 1979. The theory of speciation via the founder principle. *Genetics* 94:1011-1038.
- ten Kate HFC. 1884. Matériaux pour servir à l'anthropologie de la presqu'île californienne. *Bulletins Mém Soc d'Anthro de Paris* 7:551-569.
- Trinkaus E. 1981. Neanderthal limb proportions and cold adaptation. In *Aspects of Human Evolution*, edited by Stringer CB, 187-224. London: Taylor & Francis.
- Trinkaus E, Churchill SE, Ruff CB. 1994. Postcranial robusticity in *Homo*. II: humeral bilateral asymmetry and bone plasticity. *Am J Phys Anth* 93:1-34.
- Tyson R. 1975. A report of the skeletal material from the Central Desert area of Baja California, Mexico. *Actas del XLI Con Int American*, 103-115.
- Tyson R. 1977. Human skeletal material from the Cape Region of Baja California, Mexico: the American collections. *J Soc Américan* 64:167-181.

Ubelaker DH. 1999. Human skeletal remains: excavation, analysis, interpretation. 3<sup>rd</sup> edition. Taraxacum, Washington D.C.

Van Devender TR, Burgess TL, Piper JW, Turner RM. 1994. Paleoclimatic implications of Holocene plant remains from the Sierra Bacha, Sonora, Mexico. Quatern Res 41:99-108.

Van Loon AF, et al. 2016. Drought in the Anthropocene. Nat Geosci 9:89-91.

Venegas M. 1759. A natural and civil history of California. 2 vols. James Rivington and James Fletcher, London.

Veth P. 1995. Aridity and settlement in northwest Australia. Antiq 69:733-746.

Vizcaíno S. 1596. Relation of Sebastian Vizcaino: August-November 1596. 1990, translated by M. Mathes, in Ethnology of the Baja California Indians, Mathes M, ed. 135-144. Spanish Borerland Sourcebooks 5. Garland Publishing, New York.

Weisler M, Kirch PV. 1985. The structure of settlement space in a Polynesian chiefdom: Kawela, Molokai, Hawaiian Islands. New Zeal J Arch 7:129-158.

Weiss E. 2003. Effects of rowing on humeral strength. Am J Phys Anth 121:293-302.

Wescott DJ. 2006. Effect of mobility on femur midshaft external shape and robusticity. Am J Phys Anth 130:201-213.

Wescott DJ, Cunningham DL. 2006. Temporal changes in Arikara humeral and femoral cross-sectioanl geometry associated with horticultural intensification. J Arch Sci 33:1022-1036.

## **CHAPTER 5:**

### **CONCLUSION**

“If we take organic productions of a small island... we have, in their relations and affinities—in the fact that they are *there* and others are *not* there, a problem which involves all the migrations of these species and their ancestral forms—all the vicissitudes of climate and all the changes of sea and land which have affected those migrations—the whole series of actions and reactions which have determined the preservation of some forms and the extinction of others...” – Wallace (1880; p. 7 – Island Life).

This dissertation demonstrates that by contextualizing the insular organism with its ancestral evolutionary niche in the mainland, deeper insights are gained when interpreting body size and shape variation on islands. This is because the island rule explains alterations to body size in island ecologies that involve a release from a mainland selective pressure and the introduction to a novel island one. Alterations of a body size on an island is highly contextual and requires understanding the function it served in a mainland ecology and the subsequent island evolutionary pressures it's confronted with. Simple, or reductive, explanations that describe organismal body size and shape as solely responsive to carrying capacity of an island do not align with the empirical data reviewed and presented in this dissertation.

The contextuality of island evolution was demonstrated in the analyses of island biogeography of body size of primates; body proportion alterations in omnivorous foxes; and body size, shape, and robusticity of two peninsular human populations with distinct

maritime adaptations. In each chapter, I integrated aspects of island ecology with measures of body size variation to illuminate the diversity of evolutionary responses among populations. In doing so, I added important empirical data to aid in theoretical developments within island science but also in skeletal and evolutionary biology. These theoretical, methodological, and empirical contributions offer anthropologists a valuable new framework to assess population variation of diverse primate taxa in response to island areas and hopefully aid in the re-calibration of the island rule.

I propose a re-alignment with the island rule within biological anthropology such that the following components are used to assess body size and shape variation as a response to islands: isolation by distance from ancestral populations and population-resource dynamics. Isolation by distance is a measure of the ecogeographic boundary that was migrated over to colonize an isolated area. It reflects limits to immigration and emigration in the isolated area and the effect that these limits have on population variation. Variables such as spatial (km) and temporal (years) distance are suitable for assessing isolation by distance and depend on the types of research questions. For instance, spatial distance is more reflective of the effects of immigrant selection on the resultant isolated population, whereas temporal distance can assess the effects that genetic drift or selection within the island area influence the phenotype.

Population-resource dynamics reflect how a population is responding to the novel island environment. While research has identified that character displacement due to the lack of community members and predators significantly influence hippo and elephant body sizes on islands, population pressures for primates may be more significant. Population pressures relating to mortality rates and investment tradeoffs to survive and

reproduce within a sociocultural niche may act to influence body sizes among primates more so than the presence or absence of other species. Last, resource dynamics is how an organism is obtaining resources and interacting with other members of the population and community. By contextualizing the population dynamics with the types of resources they are interacting with on the mainland verse island, insights can be gained on the types of selective pressures that are shaping body size in island ecologies.

Integrating new waves of thinking into a discipline takes time, and for anthropology, usually comes with some resistance as humans (and often hominins) are viewed as being particularly immune to the ecogeographic constraints that commonly influence other mammals. For instance, Neandertal (*Homo neanderthalensis*; King, 1856) variation was described as pathological (Virchow, 1872; Schultz, 2009) until anthropologists analyzed the fossils with appreciation of ecogeographic patterns of non-hominin variation of body form in cold climates (Coon, 1962). This came almost a century after phenotypic responses to climate and latitude were observed in other mammals (Bergmann, 1847; Allen, 1877). The large body mass and short limbs with low intramembral indices conform with Bergmann's (1847) and Allen's Rules (1877) where organisms have decreased surface area to volume ratio in cold climates (Ruff, 1994). Application of these rules are now so entrenched within the discipline that they often are used as a theoretical starting point to assess variation in human body size and shape (Holliday, 1997; Trinkaus, 1981; Katzmarzyk and Leonard, 1998; Ruff, 2002; Kurki et al., 2008; Temple and Matsumura, 2011; Auerbach, 2012; Cowgill et al., 2012; Roseman and Auerbach, 2015).

## Literature Cited

- Allen JA. 1877. The influence of physical conditions in the genesis of species. *Rad Rev* 1:108-140.
- Auerbach B. 2012. Skeletal variation among early Holocene North American humans: implications for origins and diversity in the Americas. *Am J Phys Anth* 169:525-536.
- Bergmann C. 1847. About the relationships between heat conservation and body size of animals. *Goett Stud* 1:595-708.
- Coon CS. 1962. The origin of races.
- Cowgill LW, Eleazer CD, Auerbach BM, Temple DH, Okazaki K. 2012. Developmental variation in ecogeographic body proportions. *Am J Phys Anth* 148:557-570.
- Holliday TW. 1997. Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evo* 32:423-447.
- Katzmarzyk P, Leonard WR. 1998. Climatic influences on human body size and proportions: ecological adaptations and secular trends. *Am J Phys Anth* 106:483-503.
- King W. 1864. The Reputed Neanderthal Fossil Man. In: *Quart J Sci. Band 1 S.* 88–97.
- Kurki HK, Ginter JK, Stock JT, Pfeiffer S. 2008. Adult proportionality in small-bodied foragers: a test of ecogeographic expectations. *Am J Phys Anth* 136:28–38.
- Roseman C, Auerbach B. 2015. Ecogeography, genetics, and the evolution of human body form. *J Hum Evo* 78:80-90.
- Ruff C. 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearb Phys Anthropol* 37:65-107.
- Ruff C. 2002. Variation in human body size and shape. *Annual Review of Anthropology* 31:211-232.
- Schultz M. 2008. Rudolf Virchow. *Emerg Inf Dis* 14:1480.

- Temple DH, Matsumura H. 2011. Do body proportions among Jomon foragers from Hokkaido conform to ecogeographic expectations? Evolutionary implications of body size and shape among northerly hunter-gatherers. *Int J Osteoarchaeol* 21:268-282.
- Trinkaus E. 1981. Neanderthal limb proportions and cold adaptation. In *Aspects of Human Evolution*, edited by Stringer CB, 187-224. London: Taylor & Francis.
- Virchow RLK. Cellular pathology, 1859 special ed., 204–207. London: John Churchill.
- Wallace AW. 1880. *Island Life*. University of Chicago Press, USA.

## VITA

Colleen B. Young was born and raised in Los Angeles, California. She attended Cuesta Community College where she developed a passion for Anthropology. In 2009, she transferred to UC Berkeley where she worked in the Human Evolution Research Center under Dr. Tim White. Here, she developed and shaped her interests in island evolution and human paleontology. She also worked with Drs. Anthony Barnosky and Emily Lindsey on biodiversity and a tar pit excavation in Ecuador where she developed her skills on international collaboration. Under the advisement of Drs. Patrick Kirch and Kent Lightfoot, she researched zooarchaeological specimens from a Late Holocene Chumash site on Santa Cruz Island, California (SCrI-100), for her senior honors thesis. She also fought to keep the anthropology library open and was a prominent activist on campus. The culmination of her passion for education, dedication to research, and high grade point average resulted in her winning the Ted McCown scholarship, departmental recognition, and highest honors at graduation.

In 2023, she moved to the University of Missouri-Columbia to work with Dr. Libby Cowgill on understanding ecogeographic variation and evolution of humans on islands. Here, she received a National Science Foundation Graduate Research Fellowship and Graduate Research Opportunities Worldwide awards. She used these funds to travel to museums in California, New York, Michigan, and the Bahamas, where she amassed a large database of skeletal size and shape of human and nonhumans on islands. In 2015, she drove down the entire Baja California peninsula and lived in La Paz to work with local archaeologists and gather data on skeletal remains in the region. She identified, measured, and analyzed several archaeological sites for the region and provided outreach.

In 2018 and 2019, she visited the museum in Mexico City where she was able to meet her family from Mexico City and collect data on skeletal remains from the Cape Region.

These opportunities and experiences have contributed to her expertise on Baja California paleobiology, island evolution of body size and shape, and museum curation.

While at Mizzou, she prevented cuts to graduate health insurance but organizing a strike and helped form the Forum on Graduate Rights and Union for graduate students. Further, she worked at the St. Louis Science Center as an educator in the Ecology and Environment Gallery. She is passionate about public access and inclusion to science and the scientific process.