Human Self-Domestication by Intersexual Selection: Female Social Status and Stature Sexual Dimorphism

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I hereby declare that, except where it is otherwise acknowledged in the text, this thesis represents my own original work. All versions of the submitted thesis (regardless of submission type) are identical.

Signed: ________________________________

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Abstract

This research examines one of the three primary mechanisms currently proposed to explain apparent self-domestication in *Homo sapiens*—that is, intersexual selection against reactive aggression. My central hypothesis is that human self-domestication has been, at least in part, caused by context-dependent female preferences for less-aggressive males. Following from this, I expect that societies where women have both higher social status and secure access to nutritional resources will tend to show relatively elevated signs of human self-domestication—as indicated by lower stature sexual dimorphism. In essence, I predict an interaction between female status and food security in shaping stature sexual dimorphism.

To facilitate a cross-cultural test of my functional hypothesis, I collected male and female stature data for 92 of the 186 societies in the Standard Cross-Cultural Sample. These data allowed for a multivariate-regression, multimodel-inference analysis of the relationship between stature sexual dimorphism, and female social status and food security. Controlling for confounding factors such as shared cultural ancestry and mean body size, the analysis revealed strong evidence for the hypothesized interaction between the two predictors of interest in shaping the outcome variable.

Overall, this study expands upon the findings of several previous investigations into human stature sexual dimorphism, whilst contradicting some others and providing directions for further investigation. The principle conclusion of this work is that context-dependent female mate choices significantly contribute to a lessening of stature sexual dimorphism and, therefore, are likely to have played an important role in the self-domestication of our species.

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Chapter 1:

Introduction

1.1. Problem Statement

Domesticated species share multiple behavioural, physiological and morphological characteristics, collectively referred to as ‘domestication syndrome’ (Darwin, 1868; Hemmer, 1990; Leach, 2007; Wilkins, Wrangham, and Tecumseh Fitch, 2014). This syndrome has been shown to emerge following selection for lower levels of reactive aggression (Trut, 1999; Trut et al. 2001; Trut et al., 2006). This form of aggression is associated with instinctive, or ‘fight or flight’, type reactivity and violence, and can be contrasted with forms of pro-active (or ‘predatory’) aggression, which involve deliberate, non-reactive, violent actions (Weinshenker and Siegel, 2002; Wrangham, 2014).

Our own species, *Homo sapiens*, shows evidence of domestication syndrome, leading to the suggestion that modern humans are a ‘self-domesticated’ hominin (Groves, 1999; Leach, 2003; Franciscus et al. 2013; Cieri, et al. 2014; Wrangham, 2014; Hare, 2016). Further, it has been suggested that the self-domestication process was essential to the development of complex shared culture and technological exchange that provides the foundation for all human civilisations (Cieri et al., 2014; Hare, 2016).

Three primary mechanisms have been proposed as potential drivers of human self-domestication, these are:

1. Generalised social benefits which promote higher reproductive fitness for less aggressive, hence more cooperative, individuals in high-density populations (Cieri et al., 2014).
2. Collective advantages for members of groups that repeatedly ostracise excessively-aggressive individuals thereby preventing their contribution to succeeding generations (Pinker, 2011; Wrangham, 2014).
3. Intersexual selection via sustained female choice for less-aggressive mates, who are more likely to invest energy and resources towards shared parenting effort (Cieri et al., 2014).

In this study I examine the third potential driver of human self-domestication by statistically analysing cross-cultural ethnographic information and body size sexual dimorphism (a characteristic known to be influenced by the domestication process (Zeder, 2008, 2012)). I do so on the basis of the dual premise that in order to select for less aggressive males, women must have both a capacity to choose, and a preference for less-aggressive male partners.

I expect that female capacity to choose will be higher in societies where women maintain relatively high social status. However, female preference for less-aggressive males should vary according to relative availability of necessary resources (Brooks et al., 2010). Given these expectations, I hypothesise that low stature sexual dimorphism (as an indicator of relative self-domestication) will occur in societies with both higher female social status *and* relatively secure food resources (i.e., these predictors will interact in shaping the outcome variable of stature sexual dimorphism). To test this hypothesis, I use multiple regression analysis and multi-model inference with data on stature sexual dimorphism, female social status, and food resource security from 92 of the 186 societies in the Standard Cross-Cultural Sample (Murdock and White, 1969).

1.2. Significance

This study addresses an important area in current anthropological research by providing comparative evidence of relevance to understanding the evolutionary mechanisms driving human self-domestication. A decline in previous levels of reactive aggression is thought to have allowed the development of capacities for cooperation, knowledge sharing, and culture that underpin all human societies and civilisations (Cieri et al., 2014; Hare, 2016). As such, understanding the mechanisms behind this decline represents an important opportunity for significant research in human behavioural ecology, and in biological anthropology more generally. By providing an empirical investigation of the role played by intersexual selection in the recent evolution of human sociability and cooperation, this study makes a significant contribution to a scientific understanding of the underpinnings of human biology and society. Furthermore, given its focus on female social status and nutritional security, my research contributes to knowledge in a number of cognate fields (development studies, gender politics, cultural anthropology, and others), and may inform evidence-based policy related to female social status across a range of modern socio-economic environments.

1.3. Organisation of Thesis

Chapter 1 (‘Introduction’) presents the research problem, including a clear statement of the overarching hypothesis. Chapter 2 (‘Literature Review’) provides background information related to this hypothesis. It includes detailed discussions of the comparative method, the self-domestication hypothesis, previous explanations of stature sexual dimorphism, and an introduction to theories associated with intersexual selection in humans. Chapter 3 (‘Methods’) provides an account of the methods used, including the sources of morphological and cultural data, as well as analytical techniques employed to test the specific prediction derived from the hypothesis. Chapter 4 (‘Results’) provides descriptive statistics for the sample, as well as the results of multivariate analyses. Chapter 5 (‘Discussion’) contextualises the results in terms of existing literature, and also discusses the limitations of this study. Finally, Chapter 6 (‘Conclusion’) summarises the thesis and provides some suggestions for further research.

Chapter 2:

Literature Review

This chapter provides a background for both the methodological approach—using comparative methods with cross-cultural data to test functional (i.e., adaptive) hypotheses about human behaviour and biology—and the theoretical foundation for this work—reviewing the literature on domestication, self-domestication, sexual dimorphism, and intersexual selection in humans.

2.1. Comparative Cross-Cultural Studies

As a comparative study, my thesis uses existing ethnographic and morphological data to test functional hypotheses about the relationship between variables presumed to have a causal relationship. The core premise to be examined is that variation in mean stature sexual dimorphism between human societies can be explained by corresponding variation in cultural and environmental factors associated with female social status and food security.

Experimental approaches are a commonly posited alternative to comparative methods (Davies et al. 2012; Thornhill and Fincher, 2013). The former involve the creation of controlled situations where observation and testing of response following deliberate manipulation, or ‘treatment’, can be performed. In experimental research, the ideal comparison is between artificial treatment conditions and observed responses within a given variable, whilst explicitly comparative methods, such as those applied here, use data gathered under pre-existing conditions without resort to an artificially controlled observational environment. Despite the methodological contrasts between these two approaches however, both inevitably rely upon the observation of correlations between measured outcomes and specified influential variables which are always assessed using statistical comparison.

Given this logical similarity, the only effective difference between the two approaches is in how they control for potentially confounding influences (Thornhill and Fincher, 2013). Experimental approaches moderate these by either eliminating them from the test situation altogether, or by setting a specific level of influence and ensuring equal conditions are applied to all subjects. By contrast, comparative methods use statistical controls, which achieve the same aim by mathematically testing the measurable response under varied levels of influence from predictor and control variables. Either way, the inferential strength of each method relies entirely upon the capacity of the researcher to identify potentially confounding influences and include them as variables within the analysis (Thornhill and Fincher, 2013).

One well-documented way in which the results of investigations may be confounded is via phylogenetic relation between cases—referred to as 'Galton's problem' (Naroll, 1961, 1965). This situation occurs where similarities between observed cases are due to close phylogenetic relationship to an ancestral group, which suggests that observations cannot be treated as independent for the purpose of statistical analysis (Naroll, 1961, 1965; Felsenstein, 1985; Davies et al., 2012). This issue is not confined to comparative approaches. However, it is thought to be particularly problematic for this methodology and has been especially associated with its application to cross-cultural research, in part because it was first introduced in this context (Naroll, 1965).

Phylogenetic controls have been widely suggested to provide the best means of managing potential confounding via this form of non-independence (Felsenstein, 1985; Nunn and Barton, 2001; Freckleton, 2009). These have become a common technique used in association with cross-cultural comparisons in biological anthropology (e.g. Holden, 1999; Holden and Mace, 1999; Gustafsson and Lindenfors, 2009). However, the need for such controls has recently been questioned in commentary by Thornhill and Fincher (2013), who suggest that where the subject of investigation is the maintenance (as opposed to the origin) of cultural correlations, phylogenetic descent is theoretically and practically irrelevant. For instance, if a trait emerged in an ancestral group in response to a particular ecological variable, its persistence within any descendant groups is more likely to rely upon the continued influence of the relevant causative variable, rather than simply evolutionary inertia in the absence of this initial impetus. Thornhill and Fincher (2013) argue that the cause of origin in a trait is entirely separate to the cause of its maintenance, and that both of these causes may be legitimately investigated; whether in concert, or in isolation.

In the present example where we hypothesise that low stature sexual dimorphism is a result of intersexual selection against aggression, the question is not whether any correlation between cultural norms and biological characteristics (such as sexual dimorphism) arose independently, it is whether a relation between these factors is maintained across various, recognisably distinct, social milieus. Given significant variation in the ratio of stature sexual dimorphism across human societies, and the notable permutations of cultural tradition between even closely-related groups, the fact of phylogenetic relationship is unlikely to influence the common maintenance of an association between these factors.

Despite this argument however, it is now common practice within cross-cultural analyses to control for phylogenetic relation in some way, and various statistical methods have been proposed to do so (e.g. Naroll, 1961; Felsenstein, 1985). Previous investigations of variation in human stature sexual dimorphism have used detailed phylogenic controls (for instance: Holden, 1999; Holden and Mace, 1999; Gustafsson and Lindenfors, 2009). Similarly, the present study has controlled for Galton's problem; and it does so in two main ways: One of these is through its use of the Standard Cross-Cultural Sample (Murdock and White, 1969). The other is via robust statistical techniques involving clustering based on different world regions.

The original purpose of the Standard Cross-Cultural Sample was to alleviate the confounding effects of shared phylogeny. It was constructed by Murdock and White by selecting specific, well-described, societies from the pre-existing Ethnographic Atlas (developed earlier by Murdock, 1967). This new sub-collection of cultural groups was systematically chosen from across 200 global sub-regions to avoid phylogenetic relation and to provide a useful representation of humanity's extreme cultural diversity. As such, the use of this particular database entails a level of phylogenetic control and systematic independence of observations from the outset. Over and above this inbuilt level of phylogenetic independence, the present study also applies statistical controls for proximity between societies by clustering on the six world regions (variable 200) that are coded for within the sample (Chapter 3).

2.2. Domestication Syndrome: Symptoms and Causes

In this section of the thesis I introduce existing theory and evidence regarding mammalian domestication syndrome as well as the process of self-domestication in humans. I begin by providing an overview of research related to the apparent symptoms of domestication, and their known cause, sustained selection against aggression. I then introduce a case-study of 'self-domestication' within a wild non-human primate, the bonobo (*Pan paniscus*), and provide evidence for a similar process in modern humans. Following this, I discuss the use of stature sexual dimorphism as an indicator of relative self-domestication across different human populations, and survey some alternative explanations for variability in this trait. Finally, I outline literature related to female mate choice as a mechanism for selection against aggression in humans, and elaborate the specific hypothesis and prediction examined in this thesis.

2.2.1. Animal Domestication Induced by Humans

Charles Darwin (1868) was the first author to describe a range of morphological, physiological and behavioural traits shared among commonly domesticated species. Darwin was keenly interested in the results of deliberate human selection of these animals and this research formed part of the early evidence for evolution by natural selection (Darwin, 1859). Since this initial work, multiple authors have confirmed and extended Darwin's observations (see Hemmer, 1990; Leach, 2003). The observed suite of domesticated characteristics (Table 2.1) is now commonly described as 'domestication syndrome' (Wilkins et al., 2014). Each of these heritable modifications is generally apparent when the domesticated form of a species is compared to its wild ancestor or extant non-domesticated relatives.

Whilst Darwin (1868) clearly recognised that these alterations were the result of breeding selection, he could not explain the specific selective pressures that would cause them to be so widely shared, nor was he aware of the biophysical or genetic mechanisms underlying their development. Several domesticated characteristics were particularly puzzling as it is unclear why they should be beneficial from the point of view of early human domesticators (Hemmer, 1990). However, more recently, Russian fox-breeding experiments have demonstrated that sustained selection for low reactive aggression towards human handlers causes other domesticated characteristics to emerge and spread spontaneously within a given population (Belyaev, 1979; Trut, 1999; Trut et al., 2001, 2006). Among the domesticated foxes, these observed characteristics included: lower sexual dimorphism, facial shortening (less prognathism), altered coat pigmentation and pattern, floppy ears, curly tails, and biannual and non-seasonal oestrus (Trut, 1999; Trut et al., 2006).

Table 2.1. List of traits associated with domestication syndrome in mammals.

Trait	**Associated Symptoms**	**References**
Less aggression	Lower reactive aggression and stress responses	(Hemmer, 1990; Trut, 1999; Trut et al., 2006; Wilkins et al., 2014)
Lower sexual dimorphism	Diminished body-size, cranial, and canine sexual dimorphism	(Hemmer, 1990; Zeder, 2008, 2012; Zohary, Tchernov, and Horwitz, 1998)
Shorter nose or snout	Lower prognathism in craniofacial structure	(Hemmer, 1990; Wilkins et al., 2014; Cieri et al., 2014; Zeder, 2008, 2012; Leach, 2003)
Reduced cranial capacity	Smaller brains and reduced cranial capacity	(Hare, Wobber, and Wrangham, 2012; Kruska, 2005; Wilkins et al., 2014)
More gracile skeleton	Less-robust skeletal structure and morphology	(Hemmer, 1990; Wrangham and Pilbeam, 2001)
Smaller teeth	Reduced tooth size	(Darwin, 1868; J. Clutton-Brock, 1999; Wilkins et al., 2014)
Paedomorphic traits	Ancestral juvenile characters retained by descendant adults	(Hare et al., 2012; Trut, 1999)
Altered sexual receptivity	Non-seasonal oestrus and increased sexual behaviour and reproduction	(Kruska, 1988; Trut, 1999; Hare et al., 2012)
Altered pigmentation	Altered pelage and skin pigmentation	(Darwin, 1868; Hemmer, 1990; Wilkins et al., 2014)
Softened outer ear structure	Ears become ‘floppy’ with less cartilage	(Darwin, 1868; Wilkins et al., 2014)

This experimental evidence demonstrated that selection solely on the basis of less-aggressive behaviour may inadvertently stimulate many of the morphological and physiological side effects observed among traditional animal domesticates. The experiment also confirmed that the presence of domesticated morphology is a reliable predictor for less aggressive, more sociable, behaviours within an individual (Trut et al., 2006), a phenomenon previously noted and discussed by other authors (e.g. Hemmer, 1990).

It has since been identified that the physiological mechanism linking behaviour, morphology, and physiology under domestication is the diminishment of neural crest cell function—either via lesser overall quantity, or by restricted transport of these cells (Wilkins, Wrangham, & Tecumseh Fitch, 2014). After completing their functional role in forming the embryonic neural tube, neural crest cells are transported to other locations within the developing organism where they contribute to multiple, otherwise unrelated, biophysical features and structures (Huang & Saint-Jeannet, 2004; Dupin & Sommer, 2012; Wilkins et al., 2014). For instance, they provide the primary cellular material for bone and cartilage in much of the cranial-facial region (forming the basis of jaws and teeth, the bones of the inner ear, the hyoid, and the larynx). Elsewhere, they contribute to bodily pigmentation and to various soft tissues and organs. Of particular importance in the case of domestication, they provide the basis for development of the adrenal medulla and sympathetic ganglia which are both implicated in reactive behavioural responses (Wilkins et al., 2014). Given the diverse roles of neural crest cells, modification of their function will alter the development of other biophysical structures and may influence fundamental ontogenetic and physiological development within a given lineage.

It follows from the above that the domestication process proceeds in response to behavioural selection against reactive aggression via heritable reduction in the size of the adrenal system—a trait previously noted among domesticated animals (Hemmer, 1990). This, in turn, is caused by a diminishment in the function or dispersal of embryonic neural crest cells, (Wilkins et al., 2014). However, due to the diverse functional roles of neural crest cells, selection for less aggression also promotes a range of other modifications in domesticated physiology and morphology. The maintenance of these modifications in subsequent generations indicates a heritable genetic basis for these changes, however, multiple genes may influence neural crest cell functioning, and different combinations of genes are likely to be responsible for domestication within each species (Wilkins et al., 2014). This may explain the apparent variation in traits between different domesticated taxa.

2.2.2. Self-Domestication in a Wild Primate

Hare et al. (2012) recently compared aspects of bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) morphology, behaviour, and physiology, and concluded that wild bonobos possess many traits commonly associated with domestication. These traits include: lower reactive aggression, less intergroup violence, and diminished predatory behaviour (Kano, 1992; Hare, 2009; Furuichi, 2011; Hare et al., 2012; Surbeck and Hohmann, 2013; White et al. 2013; Gruber and Clay, 2016); lower levels of sexual dimorphism (Shea, 1983; Surbeck and Hohmann, 2013); reduced cranial capacity (White, 1996; Hare et al., 2012); smaller canine teeth (White, 1996; Hare et al., 2012; Surbeck and Hohmann, 2013); paedomorphic morphology—i.e. the retention of juvenile morphological traits (pale tail-tuft and depigmented lips) into adulthood (White, 1996; Hare et al., 2012; Gruber and Clay, 2016); paedomorphic behaviour—i.e. adult climbing behaviours, adult play, and increased sexual interaction (Doran, 1992; Hare et al., 2012); altered male testosterone levels (Surbeck et al. 2012; Wobber et al. 2013); and an extended oestrus and ‘pseudo-oestrus’ cycle in females (Furuichi, 2011; Gruber and Clay, 2016).

The two extent species of *Pan* diverged approximately 1-2 million years ago and have been separated by the Congo River since that time (Rilling et al., 2011; White et al., 2013; Gruber and Clay, 2016). There has been conspicuous debate among primatologists concerning the divergent traits of *P. paniscus* and *P. troglodytes,* especially in regard to various social behaviours and levels of aggression (Stanford, 1998; Wrangham and Pilbeam, 2001). These debates draw significant interest, in part, because the two Panins are *Homo sapiens'* nearest extant relatives and are, therefore, expected to inform inferential models with regard to the behaviour of our common ancestor and of early humans (Stanford, 1998; Gruber and Clay, 2016).

As an explanation for domestication syndrome within this otherwise-wild primate, Hare et al. (2012) suggest that a form of 'self-domestication' must have occurred. Given that sustained selection against reactive aggression provides the impetus for domestication in other species, they propose that a similar process has operated in *Pan paniscus*. This led to the expectation that the elevated level of bonding between female bonobos, and the increased social status that this confers (relative to that of female chimpanzees), have both facilitated an increased level of intersexual selection for less aggressive males (Hare, Wobber, & Wrangham, 2012). Higher female social status is expected to raise the relative influence of female mate preferences because high status females are less likely to be sexually coerced by males and, therefore, are able to exercise a higher degree of mate choice than occurs among chimpanzees (Furuichi, 2011; Hare et al., 2012; Tokuyama and Furuichi, 2016). Given female ability to avoid coercion, along with a preference for lower aggression in male partners, aggressive male behaviour has ceased to provide any significant reproductive advantage (Tokuyama and Furuichi, 2016). Over time, this situation is expected to have promoted lower levels of aggression and the consequent emergence of domestication syndrome throughout the species as a whole.

2.2.3. Self-Domestication in Humans

Following Darwin's observations regarding domestication in non-human animals, multiple authors have considered the potential for past self-domestication within our own species, *Homo sapiens* (Fischer, 1914; Lorenz, 1940; Groves, 1999; Leach, 2003;

Brüne, 2007). Recent scientific discourse has re-focused attention upon on this topic (Cieri et al., 2014; Franciscus et al., 2013; Wrangham, 2014; Hare, 2016).

Relative to our earliest ancestors, evidence for human self-domestication includes: reduced body size and increased skeletal gracility (Ruff, 2002; Ryan and Shaw, 2015) less sexual size dimorphism (Frayer, 1980; Frayer and Wolpoff, 1985; McHenry and Coffing, 2000; Plavcan, 2012a); reduced prognathism and facial masculinity (Cieri et al., 2014); diminished cranial capacity (Wiercinski, 1979; Ruff et al. 1997; Liu et al., 2014); smaller teeth (Brace et al. Hunt, 1987), and higher levels of sociability and cooperation (Pinker, 2011; Hawkes, 2013; Cieri et al., 2014; Wrangham, 2014; Hare, 2016).

Prior to the discovery of selection against aggression as the catalyst for the emergence of domestication syndrome (Trut, 1999; Trut et al., 2006) researchers could only speculate as to the mechanisms driving apparent human self-domestication. Previous commentary tended to assume that Neolithic cultural adaptations and environmental modifications such as housing, cooked food, and fire were responsible for all domesticated traits in both non-human animals and in humans themselves (Wilson, 1991; Leach, 2007, 2003; Brüne, 2007)—this despite the appearance of domesticated morphological symptoms in humans well before the Neolithic period (Groves, 1999; Cieri et al., 2014).

Regrettably, some of the earliest hypotheses regarding human self-domestication were heavily influenced by Social Darwinism. Authors such as Fischer (1914) and Lorenz (1940) emphasised the notion that domestication was a perversion of natural selection which had led to weakness and ‘degeneration’ in *Homo sapiens.* They blamed domestication in humans for multiple modern maladies and these perspectives were influential within the eugenics movement and abhorrent social programs in many nations, including Nazi-era Germany (Brüne, 2007).

In dramatic contrast however, recent research has highlighted the beneficial aspects of elevated human sociability, and cultural transmission or 'behavioural modernity' (Sterelny, 2011, 2012), made possible through increased social tolerance, and inferred pre-historic reductions in individual reactive aggression (Pinker, 2011; Cieri et al., 2014; Wrangham, 2014; Hare, 2016). The resulting enhancement of human ability for social interaction is believed to have facilitated a dramatic increase in our capacities for cumulative knowledge sharing, and 'technological ratcheting' (Tennie et al. 2009), which enabled relatively-recent cultural sophistication in humans, including the phenomenon of complex civilisation (Sterelny, 2011, 2012; Cieri et al., 2014; Hare, 2016).

Analysis of preserved craniofacial material has demonstrated a decrease in the morphological indications of circulatory testosterone (e.g. smaller brow-ridges and reduced facial width-to-height ratios) since the first emergence of early *Homo sapiens* (Cieri et al., 2014). Because testosterone is also linked to levels of aggressive behaviour (Nelson and Trainor, 2007; Goetz et al., 2014), this change in morphology further suggests a decline in reactive aggression over the past 200,000 years (Cieri et al., 2014). Given this diminishing trend in aggression, we may expect other traits of domestication (Table 2.1) to have emerged over this time period, and indeed, as outlined above, the fossil record provides evidence for multiple morphological trends that are consistent with a process of human self-domestication. One particularly useful indicator of domestication is a reduction in body-size sexual dimorphism (Zohary et al., 1998; Zeder, 2008, 2012), and humans show consistent reduction in this trait from the Late Pleistocene: a reduction caused by decline in body size among males (Frayer, 1980; Frayer and Wolpoff, 1985; Ruff, 2002; Hill et al. 2017).

2.2.4. Evolutionary Perspectives on Size Sexual Dimorphism

The term ‘sexual dimorphism’ typically describes any secondary difference between males and females of a given species, beyond the primary differences that occur in reproductive gametes and associated sexual organs (Plavcan, 2001; T. H. Clutton-Brock, 2007). Sexual dimorphisms occur across the majority of taxa and include: divergent body sizes and shapes; the presence of visible features, such as antlers and spurs, and more brightly-coloured skin, fur, or feathers; as well as multiple other structural and physiological differences. These traits are typically associated with sexually differentiated behaviour appropriate to divergent mating or resource exploitation strategies (Ralls, 1976; Slatkin, 1984).

Darwin (1871) was particularly interested in the phenomenon of sexual dimorphism, and was—naturally enough—one of the first to provide an evolutionary explanation for it. Initially, he found the existence of some dimorphic traits problematic with regard to the theory of natural selection since they seemed disconnected from primary selective pressures associated with resource competition and survival (Davies et al., 2012). The explanation he later formulated for these traits was termed ‘sexual selection’ (Darwin, 1871), an idea elaborated into two primary forms: intrasexual and intersexual.

Intrasexual selection occurs where selection is directly due to competition between members of the same sex, usually for relatively limited mating opportunities, although sometimes for resources that are indirectly associated with reproductive success (Ralls, 1976). This primarily takes place as contest competition, typically between males, and entails direct physical competition for dominance where this leads to increased mating opportunity. It is likely to lead to male adaptations which provide advantages in physical combat or intimidatory display, such as large body-size and increased muscle mass (Puts, 2010, 2016; Hill et al., 2017). It may also occur through sperm competition, which is likely to evolve if contest or coercion cannot ensure effective monopolisation of females (Puts, 2016).

By contrast, intersexual selection is where one sex selects mating partners based on their possession of a certain desirable trait, or traits (Andersson, 1982; Davies et al., 2012; Hill et al., 2017). This generally leads to significant increase in, or elaboration of, the trait in question. This second form of selection is particularly noted among avian species, where one of the sexes (most often the male) is sexually selected to possess extreme forms of secondary sexual characteristics such as: a long tail, brightly-coloured feathers, the ability to construct a well-decorated bower, or virtuoso capacity for song, or dance (Andersson, 1982; Borgia, 1986; Davies et al., 2012).

Each of these modes of sexual selection has specific implications in regard to likely evolutionary outcomes for the sexes of a given species. Trivers (1972), following earlier work by Bateman (1948), proposed a general mechanism to explain the occurrence and typical outcome of sexual selection. This model predicts that in any species, the members of the sex which invests the least effort towards the nurture of offspring will compete amongst themselves for reproductive access to the higher-investing sex. It follows therefore, that the least-investing sex of a species will evolve traits indicative of intrasexual competition and will seek to reproductively monopolise multiple individuals of the high-investing sex; whereas the higher-investing sex will tend to be more ‘choosy’ (Darwin, 1871; Trivers, 1972; Davies et al., 2012; Low, 2015). By preference, individuals of the choosier sex consent to mate with non-investing partners that display certain characteristics which are likely to confer, or, at least are associated with, survival or reproductive advantage.

Parental investment includes the provision of any beneficial effort that requires expenditure of finite parental energy or resources. It implies a trade-off between one offspring and another, or between somatic maintenance or reproductive opportunity of the parent, and the nurture of offspring (Trivers, 1972). Due largely to their defining characteristic of providing milk to dependent young, among the vast majority of mammalian taxa it is the female which invests most heavily in the nourishment and survival of offspring, whilst males tend to invest relatively less (Trivers, 1972; Davies et al., 2012; Hill et al., 2017). Following from general expectations of the model, this should predispose mammals to mating systems involving intense intrasexual selection among males, and corresponding intersexual selection via heightened choosiness among females (Darwin, 1871; Trivers, 1972). This would result in males being larger and more adapted for combat than females, and, to a large extent, this is what is generally observed—but see Ralls (1976). A common expectation is that intrasexual selection, typically via contest competition between males, leads to the development of 'armaments', which are traits useful in physical combat against other males of the same species (Emlen, 2008). On the other-hand, intersexual competition is likely to produce 'ornaments' that is, mainly superficial and non-utilitarian traits that are preferred by one sex (typically the female) as characteristics in the other (typically the male) (Andersson, 1982; Petrie et al. 1991; Davies et al., 2012).

In any given species, extreme size sexual dimorphism is widely considered as a morphological indicator of high levels of contest competition (and hence aggression) between males (T. H. Clutton-Brock et al. 1977; T. H. Clutton-Brock and Harvey, 1978; Alexander et al. 1979; Plavcan and van Schaik, 1992). There is also an associated expectation that contest competition will occur most often, and most intensely, among taxa with polygynous mating and social systems (Alexander et al., 1979; Plavcan, 2001, 2012a; but see Fuentes, 1998; and Plavcan, 2000). Consequently, there is an extensive—although far from conclusive—literature which suggests body size dimorphism is associated with polygyny in non-human animals, as well as considerable debate about whether the same should be true in humans

(Alexander et al., 1979; Gray and Wolfe, 1980; Holden and Mace, 1999; Plavcan, 2004, 2012b).

It is generally accepted that the earliest hominin species showed relatively high size sexual dimorphism (Plavcan et al. 2005). Several authors have claimed that this, in association with existing levels of sexual dimorphism in modern humans, provides an indication of strong male-male competition, hence high levels of aggression, among past and present humans (Puts, 2010; Hill et al., 2017). Despite this, it is also widely accepted that there has been a significant diminishment in hominin size sexual dimorphism since around the dawn of the first species of *Homo* (Frayer and Wolpoff, 1985; Ruff, 2002).

This trend has continued in *Homo sapiens* from the Late Pleistocene, through the Mesolithic and Neolithic, and into modern populations (Frayer, 1980; Frayer and Wolpoff, 1985; Hill et al., 2017). Two main hypotheses have been proposed to explain this decrease in size sexual dimorphism, both attempt to account for an apparent lessening in male size. The first suggests that pre-existing sexual division of labour coupled with changed hunting technology and new types of prey allowed for safer hunting, which lessened selection for large body size in males (Frayer, 1980). The second asserts that the adoption of weapons diminished selection for male biophysical armaments, such as body size, which had previously been advantageous in intrasexual contest (Hill et al., 2017). These two hypotheses are considered in further detail in the discussion section of this thesis (Chapter 5).

Despite this acknowledged prehistoric decline in human size sexual dimorphism, there remains an underlying level of height disparity between the sexes, in that males are known to be taller across all human populations (Ralls, 1976; Gaulin and Boster, 1992). Notably however, there is significant variation in the degree of this disparity between different cultural groups (Gray and Wolfe, 1980; Gaulin and Boster, 1992;

Holden and Mace, 1999; Gustafsson and Lindenfors, 2009; but see Gaulin and Boster, 1985). Multiple authors have focussed upon this variation between populations, and literature related to this particular topic is discussed in the following section.

2.2.5. Recent Stature Sexual Dimorphism in Humans

Persistent disparity in mean stature is one of a large number of sexually dimorphic human characteristics observed by researchers working across various scientific disciplines. A non-exhaustive and non-systematic sample of these sexually dimorphic human traits is presented in Table 2.2.

Table 2.2. Select sample of sexually dimorphic characteristics.

Dimorphic zone	Trait specifics and authors
Face	Variation in multiple components of the face (Samal et al. 2007), including size differences in brow ridges (Shearer, et al. 2012), as well as sexually dimorphic facial width-to-height ratios (Carré et al. 2009).
Mandible and teeth	Differences in mandibular morphology and development (Coquerelle et al., 2011) along with size and weight differences in teeth generally (Schwartz and Dean, 2005), and canines in particular (Nagesh et al. 2011).
Voice	Divergent morphology of the throat and larynx leads to differences in vocal pitch (Puts et al., 2016; Puts et al. 2006).
Post-cranial skeleton	Differences in the size and orientation of thoracic vertebra (Bastir et al. 2014) as well as the length of ribs and total volume of the rib cage (Bellemare et al. 2006).
Skull and brain	Differences in the mastoid process (Petaros et al. 2015) and basal ganglia morphology (Rijpkema et al., 2012) and size (Giedd et al. 1997) Also, olfactory function and neuron count within the olfactory bulb (Oliveira-Pinto et al., 2014). Further, life history variation in the chronology of overall brain development (Giedd et al., 1997).
Physiology	Significant and consistent differences in lipid distribution (Wells, 2012) and metabolism (Mittendorfer, 2005).

Of interest in regard to sexual dimorphism in general, is that several of the varying traits shown in Table 2.2 are also associated with divergent behavioural tendencies.

For example, facial width-to-height ratios are linked to aggressive and competitive behaviours among males (Carré et al., 2009; 2013) and male vocal pitch predicts for different levels of dominance, attractiveness, and mating success (Puts et al., 2006, 2016). These behavioural links are relevant to sexual selection processes affecting stature sexual dimorphism because they point to underlying physiological (particularly hormonal) differences that influence a suite of traits, including male stature relative to that of females.

In light of fundamental sexual selection theory, Alexander, et al. (1979) investigated whether body size sexual dimorphism is correlated with polygynous mammalian mating systems. Their work examined data from several species of pinnipeds, ungulates and primates, including humans. They found a significant correlation across the non-human species, but not, at first, when comparing contemporary monogamous and polygynous human cultural groups. On the basis that socially-imposed monogamy might artificially mask a naturally polygynous disposition in some societies, they separated monogamous cultures into 'socially' and 'ecologically' monogamous categories. Ecologically monogamous groups were defined as those where monogamy was a result of ecological constraints upon the total resources that a single male could monopolise; this was expected to impose an even distribution of wealth, and female partners, between males. Other groups were designated as 'socially monogamous' where ecological constraints were apparently absent, and monogamy was therefore assumed to be an arbitrary cultural construct. The results of further analysis showed significantly higher stature sexual dimorphism when polygynous and socially monogamous groups were compared with ecologically monogamous populations (Alexander et al., 1979).

However, these results were disputed by Gray and Wolfe (1980), who identified substantial errors in the methodology used by Alexander et al. (1979). Their own analysis found polygyny had no effect on human stature sexual dimorphism although they did find an association between polygyny and mean male stature. Despite this, they cautioned that change in this variable was just as likely due to confounding influence. As well as modes of marriage, they also considered the effect of diet and nutrition upon both male and female stature and upon stature sexual dimorphism. Since it is widely believed that male growth is more severely stunted than female growth under conditions of malnutrition, food constraints should lead to lower sexual dimorphism (Gray and Wolfe, 1980; Frayer and Wolpoff, 1985). To investigate this effect, Gray and Wolfe compared surrogate measures of protein availability to mean stature and to stature sexual dimorphism. Their findings showed that lower male stature and stature sexual dimorphism were both statistically associated with low protein availability, but, since societies with the most reliable protein availability returned both the highest and lowest stature sexual dimorphism scores, they suggest that these findings remain inconclusive. From this work, it may be noted that no definite link has been demonstrated between higher stature sexual dimorphism and polygynous marital customs, or nutritional levels (Gray and Wolfe, 1980).

Another persistent explanation for variation in stature sexual dimorphism is that it results from a simple allometric relationship to total body size, and will, therefore, shift in accord with any factor that affects the mean height of a population (Rensch, 1950; Gaulin and Boster, 1992; Wells, 2012). Work by Gustafsson and Lindenfors (2009) examined stature sexual dimorphism in light of this predicted relationship and the expectation that total body size increases in colder climates. They invoked a combination of other theories (Bergmann’s and Rensch’s rules) to hypothesise that human stature sexual dimorphism should increase along a thermocline from warmer to colder climates. Bergmann’s (1847) rule states that different populations of a single species will show increased body mass in colder climates compared to warmer ones.

Rensch's (1950) rule states that, in species where males are the larger of the two sexes, size sexual dimorphism will increase in proportion with body mass.

Accordingly, Gustafsson and Lindenfors (2009), compared climate and stature sexual dimorphism data for different human populations listed in the Ethnographic Atlas—using latitude as a substitute indicator for climate. They found that although higher male and female statures were both weakly associated with increasing distance from the equator, the statistical significance of a simple correlation between latitude and stature sexual dimorphism disappeared after controlling for phylogenetic relation (Gustafsson and Lindenfors, 2009). Despite this, they did confirm the presence of an allometric relationship whereby, in accord with Rensch's rule, stature sexual dimorphism increased with increasing mean stature.

Holden and Mace (1999) tested for associations between stature sexual dimorphism, the division of labour between the sexes, the main form of subsistence activity (hunting or agriculture), and marriage system, especially polygyny. Like Gustafsson and Lindenfors (2009), they compared cultural variables from the Ethnographic Atlas (Murdock, 1967) with stature data from various anthropometric studies. Their investigation showed no association between stature sexual dimorphism and polygyny or subsistence type, but did find that inter-group stature sexual dimorphism was negatively correlated with women's contributions to subsistence.

The implication of this finding is that women are relatively tall compared to men in societies where they contribute a higher proportion of the total subsistence requirement. Holden and Mace (1999) interpret this to mean that sex-biased parental investment was preferentially directed towards girls whenever women were more closely associated with group subsistence activities. This would imply relatively increased nutritional intake for girls in early childhood, which would maximise girls' growth relative to boys' and, hence, lead to lower stature sexual dimorphism among adults.

Although several of the studies mentioned here have disputed findings, or have returned somewhat equivocal results, this review has identified several potentially confounding variables of relevance to the present research. As such, these factors require statistical control within the comparative multivariate regression analyses performed here. From the above, these potential confounders include: absolute latitude (Bergmann, 1847; Gustafsson and Lindenfors, 2009), mean stature (Rensch, 1950), and the proportion of female contribution to subsistence (Holden and Mace, 1999). In addition to the above, work by Eveleth (1975), which found significant variation among different ethnic groups, along with the need to effectively manage Galton's problem, necessitates the inclusion of controls for phylogenetic relation. This is effectively addressed through the inclusion of variable 200, 'world region', within the final regression analyses (Section 3.4.3).

Whilst it may be contentious, the degree of monogamy or polygyny is not considered in this study due to compelling critiques of the logic behind the expectation that human marriage systems should be relevant to levels of stature sexual dimorphism within the species. The degree of dimorphism in primates shows no correlation with mating systems excepting that extreme size dimorphism may tend to indicate polygyny (Plavcan, 2000). Previous expectations that high and low sexual dimorphism were closely correlated with polygyny and monogamy respectively, are undermined by observations that many socially monogamous primates are not sexually monogamous (Reichard, 1995; Fuentes, 1998); that monogamous primates are not always monomorphic, and polygynous ones are not always dimorphic (Fuentes, 1998); and further, that sexual dimorphism is actually more closely correlated with levels of male-male competition in primates than with mating or social system per se (Plavcan and van Schaik, 1992, 1997). Added to these issues is the effective rebuttal of Alexander et al's (1979) influential study of human size sexual dimorphism by Gray and Wolfe (1980); the failure of subsequent investigation by Holden and Mace (1999) to identify any correlation between marital system and stature sexual dimorphism; and the results of Gaulin and Boster (1992) which showed higher human stature sexual dimorphism among socially monogamous populations (the opposite effect to what is generally predicted).

Furthermore, given the ritualised complexity of human courtship and marital custom, the notion that human marital arrangements, along with the extensive and varied social relationships that surround them, would predict for intrasexual selection for larger body size due to actual physical contest competition between males seems, at best, unlikely. Even if the underlying ratio of stature sexual dimorphism had been genetically pre-determined via combative intrasexual selection at some pre-historic point (suggested by Puts, 2010; Hill et al., 2017), the observed variation between present human societies (the specific focus of this present study) suggests that any underlying dimorphic predisposition would have been substantially moderated by more recent cultural or environmental influences.

2.2.6. Intersexual Selection and Human Self-Domestication

Following this review of alternative explanations for variation in stature sexual dimorphism, it seems worthwhile to briefly reiterate two important premises of the present comparative study. These are: that humans are a self-domesticated species (Cieri et al., 2014; Wrangham, 2014; Hare, 2016), and that varying levels of stature sexual dimorphism provide a measurable indication of relative self-domestication between populations (Zeder, 2008, 2012). Although one of the alternative explanations reviewed above invoked a cultural influence within sexual dimorphism outcomes, none has previously considered processes associated with mammalian domestication syndrome. Accordingly, this section of the thesis describes potential mechanisms behind intersexual selection for lower aggression among humans, and why these are relevant to our understanding of human self-domestication.

Since it is known that sustained selection for lower reactive aggression causes domestication syndrome in other mammalian domesticates (Trut, 1999; Trut et al., 2001, 2006; Wilkins et al., 2014), it may be inferred that the same selective pressure is what promoted pre-historic human self-domestication. From this, several previous authors have suggested mechanisms which might conceivably have provided sustained selection against aggression in our species. Three primary hypotheses have been proposed, these are: (1) generalized social benefits (Cieri et al., 2014); (2) collective benefits for members of groups that repeatedly ostracise excessively-aggressive individuals (Pinker, 2011; Wrangham, 2014); and, (3) intersexual selection via mate choice for less-aggressive males (Cieri et al., 2014). As discussed in Chapter 1, my thesis tests hypotheses derived from the third mechanism.

One of the main expectations in regard to evolved male and female mating preferences is that the sexes are likely to pursue distinctly divergent mating strategies (Buss, 1989; Bech-Sørensen and Pollet, 2016). According to classic research on this topic, male reproduction is predominantly constrained by the number of mating opportunities, whereas in placental mammals, such as humans, female reproduction is constrained by access to resources which support the gestation and nourishment of healthy offspring (Darwin, 1871; Bateman, 1948; Trivers, 1972). As such, women's mating preferences will often be motivated towards selecting partners who maintain a high degree of parental investment, especially by contributing nutritional resources, or other supportive benefit (Trivers, 1972; Quinlan and Quinlan, 2007). Work on sexual jealousy in males and females supports this expectation in regard to female preference, suggesting female jealousy is heavily influenced by a concern to avoid 'paternal disinvestment' (Buss et al. 1992; Stieglitz et al. 2012). Furthermore, in a cross-cultural study, Quinlan and Quinlan (2007) found low paternal investment predicted for pair-bond instability due to female defection, this implies that in societies where males contributed little to family subsistence, women were more likely to regularly seek alternative partners.

By contrast, although where males and females contribute equally to subsistence requirements, pair-bonds remain relatively stable, the highest levels of male contribution are associated with regular male defection to pursue extra-pair mating opportunity (Quinlan and Quinlan, 2007). This suggests that where males can provide highly-valued nutritional resources, they tend to use this as leverage to gain extra reproductive opportunity rather than providing extra paternal investment. In effect, choosy females face a significant conundrum due to divergence between male *capacity* to invest as opposed to their *desire* to do so. At an individual level, whilst certain males may be better able to acquire resources, these males are also more likely to pursue multiple mating opportunities (Booth and Dabbs, 1993; Kruger, 2006). Masculine (high-testosterone) men have been shown to be perceived as relatively socially dominant and more competitive, and are also more likely to achieve high social status (Kruger, 2006). However, they are also less likely to ever marry, and are more likely to engage in affairs and domestic abuse, as well as to eventually divorce, when they do marry (Booth and Dabbs, 1993).

Since testosterone affects both behaviour and morphology, women are able to estimate male behavioural tendencies via morphological cues, especially facial masculinity (Kruger, 2006; Carré et al., 2009, 2013; Lefevre et al. 2013). In keeping with divergent reproductive strategies theory, women have been shown to prefer more masculine partners in the case of short-term encounters, but less-masculine ones for long-term relationships (Kruger, 2006). That is, women will tend to select more-masculine males where there is no intention of forming a lengthy and committed relationship, but prefer relatively less-masculine males for longer-term engagements where commitment is important. Similarly, measures of women's preferences for masculine faces have been shown to be unaffected following priming with material depicting male-on-male aggression (a sign of competitive masculinity), but were significantly diminished after seeing images showing male-on-female aggression (Li et al., 2014), which might predict for low commitment and poor paternal investment.

In a meta-analysis of national indices of female preferences for masculine facial morphology, Brooks et al. (2010) demonstrated that these preferences were positively correlated with national income inequality as measured using the Gini index. That is, female preferences for masculinity were high in nation-states with higher disparity in income distribution, but were low in countries with relative wealth equality. This led Brooks et al. (2010) to conclude that where inequality exists competition for relatively constrained resources is high, and, therefore, women are more likely to prefer males who are better predisposed to social contests and dominance, since they should be better able to secure constrained resources. Conversely, it follows that women in less resource constrained environments will tend to prefer less-masculine male facial morphology because aggressive and dominating behaviours are relatively less advantageous (and therefore less desirable) in a less competitive social environment.

Given the fact that women's pre-evolved capacities for decision making are ultimately connected to the provision of nutritional resources for the nurture and growth of offspring (Trivers, 1972) rather than monetary income as measured by the Gini index (used by Brooks et al., 2010), it follows from the preceding discussion that where nutritional resources are constrained, women should tend to prefer masculine male partners who are better able to compete for available resources. Conversely, where nutritional resources are more readily available, women are more likely to prefer less-masculine (hence, less aggressive) males.

From the above elaboration of mechanisms which moderate (1) female capacity to choose, and (2) female preference for less-masculine, and less-aggressive, males, it follows that intersexual selection for lower aggression should be higher in societies where women have high social status, and where there is high and stable nutritional resource availability. Table 2.3 illustrates a matrix of outcomes based on this combination of mate choice capacity and preference. These expectations lead to the prediction that, the symptoms of human self-domestication (i.e. low stature sexual dimorphism) will be more prevalent among groups where women have both high social status (which allows capacity to choose), *and* where there is high and stable food availability (promoting a preference for less-aggressive males).

Table 2.3. Potential stature sexual dimorphism outcomes under interaction between female social status and food security.

		Female Mate Preference	
		Less Masculine Males (food constant)	**More Masculine Males (food constrained)**
Female Capacity to Choose	**Less (lower female status)**	Preference irrelevant (High dimorphism due to intrasexual selection)	Preference irrelevant (High dimorphism due to intrasexual selection)
	More (higher female status)	Low stature sexual dimorphism	High stature sexual dimorphism

Chapter 3:

Methods

3.1. Overview

In this study, I analyse stature sexual dimorphism data in association with cultural information for 92 of the 186 populations from the Standard Cross-Cultural Sample (Murdock and White, 1969). I used multiple regression analysis and multi-model inference to determine the effect of, and interaction between, female social status and food security on the level of stature sexual dimorphism for each society, while controlling for potential confounders of theoretical importance.

3.2. Data and Sample

I used the Standard Cross-Cultural Sample to obtain ethnographic data regarding female social status and food security. This database provides information on over 2000 ethnographic, geographic and environmental variables for 186 global societies (Murdock and White, 1969). These particular groups were originally systematically selected from the Ethnographic Atlas (Murdock, 1967) with the aim of ensuring maximum independence for the purpose of statistical comparison. As such, the Standard Cross-Cultural Sample provides a representative database of human societies from a range of periods in history, across different global regions, and from multiple climates and ecotypes. This minimises the effect of 'Galton's Problem' (Naroll, 1961, 1965)—the potential for spurious correlation in cross-cultural studies due to shared cultural history. For each society, the recorded ethnographic information is coded for a specific date, typically prior to any cultural disruption through European colonialism or industrialisation.

I collated data from existing anthropological and anthropometric studies on male and female height for 92 of the 186 societies in the Standard Cross-Cultural Sample (see Figure 3.1). From these data, I calculated human stature sexual dimorphism for each group. Complete information about each society in my sample, and the source of the height data, is included in Appendix 1.

To minimise sampling error, I integrated all available samples into a combined mean for each society. Where this was necessary, reports without a stated number of subjects were dropped from the overall sample. Stature data from reports that included only male, or only female, data were also avoided except in the case of the Garo, where two separate samples (one of males and one of females) were combined (Akhter et al. 2012; Jaswal, 2012). Any sample with a stated number of less than 20 individuals of either sex was excluded. Stature data provided under synonymous society names were substituted or combined. This was especially required when societies were present in the Standard Cross-Cultural Sample under one name, but listed in the anthropometric literature under a recognised synonym.

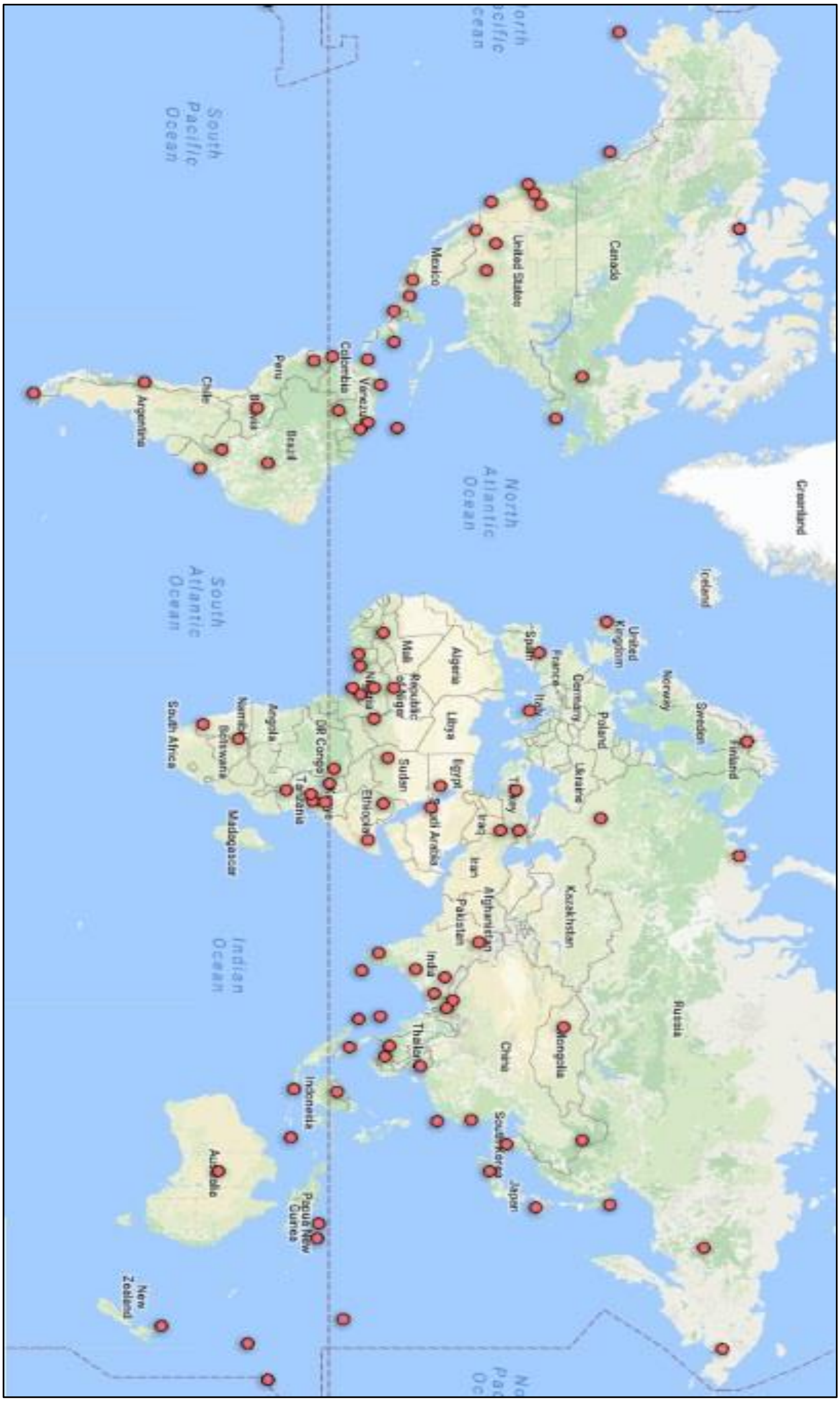

Figure 3.1. Global map showing each of the 92 cultural groups used in this study.

3.4. Variables

In this section, I describe the variables used in this study, which included one dependent variable, two predictors of interest, and four theoretically important confounding variables identified from the literature. Figure 3.2 provides a schematic illustration of each of these within the overall study design.

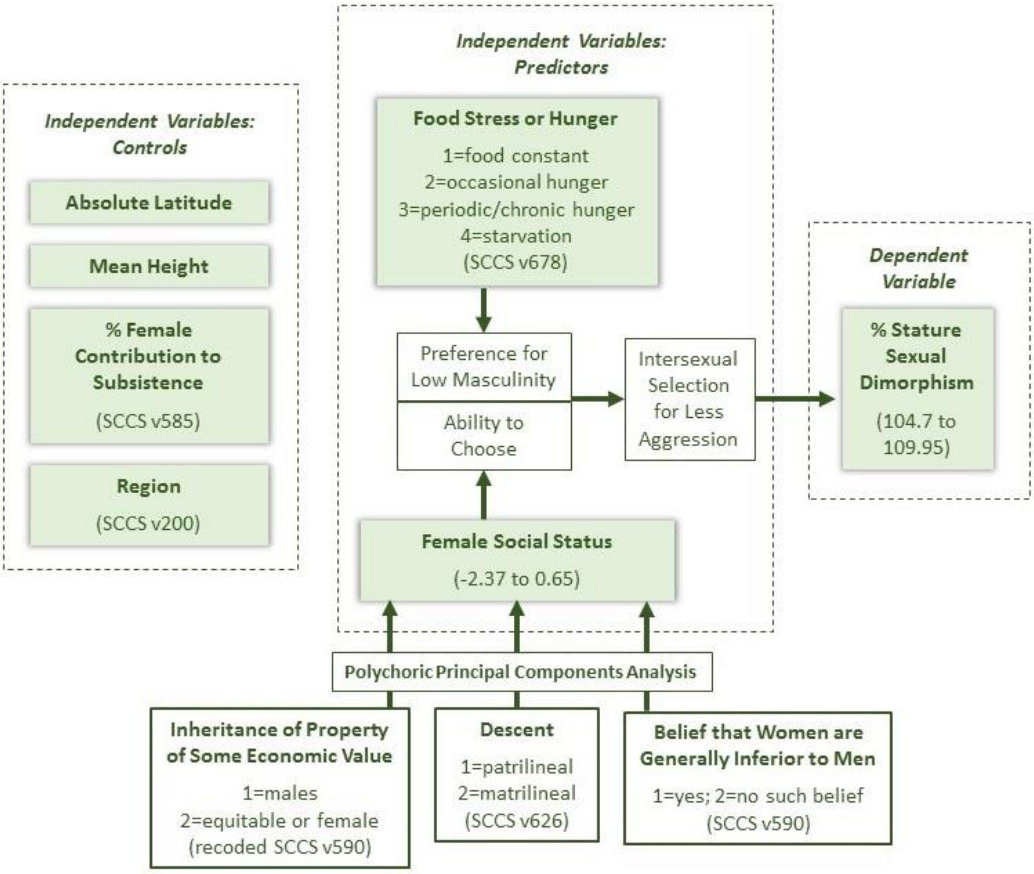

Figure 3.2. Schematic illustration of variables used in analyses.

3.4.1. Dependent Variable

I used variation in size sexual dimorphism as the dependent variable because this characteristic is known to provide a reliable morphological indicator of domestication in cultivated Neolithic mammals (Helmer et al. 2002; Zeder, 2008, 2012). Furthermore, extreme size sexual dimorphism is known to predict for high levels of male competitiveness and aggression among primates (although not for particular mating or social systems) (Plavcan & van Schaik, 1997; Plavcan, 2000, 2012). Difference in human body size may be measured as either stature or body mass. Following Alexander et al. (1979), I used stature to indicate overall size because sampled weights are susceptible to variation depending on seasonal dietary changes, fluctuating health, and stages of pregnancy. Stature sexual dimorphism scores were expressed as a simple percentage of mean male to mean female stature. Thus, a score of exactly 100 indicates no sexual dimorphism, a score of greater than 100 indicates males are larger than females, and a score of less than 100 would indicate that females are larger than males.

3.4.2. Independent Variables: Predictors

For the first predictor variable, I created an index of female social status by combining three existing variables from the Standard Cross-Cultural Sample using polychoric principal components analysis, a data-reduction tool for categorical (including binary) variables (Kolenikov and Angeles, 2009). The three variables were: (1) variable 590, 'Inheritance of Property of Some Economic Value', which was converted to binary so that 1 included 'only males' and 'male preference' and 2 represented 'equal' and 'female preference'; (2) variable 696, 'Descent', where 1 is 'patrilineal' and 2 is 'matrilineal'; and (3) variable 626, 'Belief that Women are Generally Inferior to Men', where 1 is 'yes' and 2 is 'no such belief'. The polychoric PCA was conducted using STATA 14, and yielded a first component with an eigenvalue of over 1.96 which explained 66% of the variation in the three variables. The other components yielded eigenvalues of less than 1. The resultant predictor variable has 7 unique values ranging from -2.37 (relatively low female status) to 0.65 (relatively high female status).

For the second predictor variable, I used Variable 678, ‘Food Stress or Hunger’. This ordinal variable is composed of four categories ranked from greatest to least food security: ‘food constant’, ‘occasional hunger or famine’, ‘periodic or chronic hunger’, and ‘starvation or evidence of protein deficiency’. For the purposes of this analyses, I converted the variable into a series of indicator (aka ‘dummy’) variables (Hardy, 1993). Since the available sample of stature data contained no societies ranked in the ‘starvation’ category, effectively only three categories were used in the regression analyses. ‘Food constant’ was the reference category, with ‘occasional hunger or famine’ and ‘periodic or chronic hunger’ representing increasing nutritional constraint.

I created two additional variables to test the hypothesis that the two predictors of interest interact to shape the dependent variable. Two were required rather than one because it is an interaction between a continous and a series of dummy variables (Jaccard et al. 1990; Hardy, 1993). The first interaction term was calculated by multiplying female status and ‘occasional hunger or famine.’ The second interaction term was calculated by multiplying female status and ‘periodic or chronic hunger.’ No interaction term was necessary for female status and the reference-category dummy variable, ‘food constant.’

3.4.3. Independent Variables: Controls

I selected four control variables on the basis of their potential to act as confounding influences. The first was ‘absolute latitude’, a continuous variable that measures distance from the equator, which previous studies have suggested may covary with stature sexual dimorphism (Gustafsson and Lindenfors, 2009). The second control variable was mean height, a continuous variable measured as the mean of the male and female height estimates used to measure sexual dimorphism. This was included to adjust for allometric relationship between mean height and stature sexual dimorphism—also known as Rensch’s Rule (Rensch, 1950), which is the observation that sexual dimorphism increases with increasing body size. The third control variable was percentage female contribution to subsistence (Variable 585), which has previously been shown to covary with stature sexual dimorphism (Holden and Mace, 1999). This ordinal variable was taken from the Standard Cross-Cultural Sample, but is treated as quasi-continuous in this analyses. This was considered acceptable since the underlying data was based on percentage scores; the existing ordinal scale was based on a ranking from 1-8; and results were normally distributed. The fourth and final control variable was region (Variable 200)—a categorical variable from the Standard Cross-Cultural Sample. This variable was included as a clustering variable in the multiple regression analyses to adjust for dependencies in the data due to phylogenetic relationships (i.e., 'Galton's problem').

3.5. Statistical Analysis

3.5.1. Preliminary Analyses

Before building regression models that would allow me to test my central hypothesis, I conducted two sets of preliminary analyses. First, I created a composite measure of female status using polychoric principal components analysis. I described this procedure and its outcome in Section 3.4.2 (above). Second, I regressed stature sexual dimorphism data against linear and non-linear (quadratic) forms of each of the predictors of interest and potentially confounding variables using simple linear regression to decide which form should be included in subsequent multiple regression. I assessed the results of these trials using Akaike's Information Criterion (AIC) (Akaike, 1973). I selected the best-fitting form of each variable—linear or quadratic—for use in subsequent analyses.

3.5.2. Multivariate Analysis

To test the prediction that female social status and food security interact to influence stature sexual dimorphism, while also controlling for theoretically important confounding factors, I used multiple linear regression with robust standard errors to adjust for regional clustering (Weisberg, 2005). I made special considerations for transforming categorical variables into dummy variables (Hardy, 1993), and for analysing interaction effects in regression models (Jaccard et al., 1990). To choose models for inference from amongst the candidate models, I used AIC (Aikake, 1973). My procedure included multi-model inference (Symonds and Moussalli, 2011) because the best-fitting models plus any models that had AIC values within 2 of the best-fitting model (i.e., ΔAIC<2) were considered in the results (Arnold, 2010).

In all, I considered 25 models (Table 3.1) which were constructed to provide all possible combinations of the first predictor variable, female social status, plus all other predictor and confounding variables. These combinations are described as follows:

1. Two models with all variables, including one with, and one without, the interaction terms for ‘female social status’ and the ‘food stress or hunger’ dummy variables.
2. Four models including stature sexual dimorphism and female social status paired with each of the other variables individually, plus one with the interaction terms.
3. Seven models including stature sexual dimorphism and female social status with all possible combinations of two controls, plus two with the interaction terms.

4. Five models including stature sexual dimorphism and female social status with all possible combinations of three controls, plus three with the interaction terms.

5. Two bivariate models including only stature sexual dimorphism and either of female social status, or food stress or hunger.

Table 3.1. List of 25 models assessed via AIC.

Model
Female Status +Food Stress or Hunger +Female Contribution +Latitude +Mean Stature
Female Status +Food Stress or Hunger +Female Contribution +Latitude +Mean Stature +Interaction
Female Status +Food Stress or Hunger
Female Status +Food Stress or Hunger +Interaction
Female Status +Mean Stature
Female Status +Female Contribution
Female Status +Latitude
Female Status +Food Stress or Hunger +Female Contribution
Female Status +Food Stress or Hunger +Female Contribution +Interaction
Female Status +Food Stress or Hunger +Latitude
Female Status +Food Stress or Hunger +Latitude +Interaction
Female Status +Food Stress or Hunger +Mean Stature
Female Status +Food Stress or Hunger +Mean Stature +Interaction
Female Status +Female Contribution +Mean Stature
Female Status +Female Contribution +Latitude
Female Status +Latitude +Mean Stature
Female Status +Food Stress or Hunger +Female Contribution +Mean Stature
Female Status +Food Stress or Hunger +Female Contribution +Mean Stature +Interaction
Female Status +Food Stress or Hunger +Latitude +Mean Stature
Female Status +Food Stress or Hunger +Latitude +Mean Stature +Interaction
Female Status +Food Stress or Hunger +Female Contribution +Latitude
Female Status +Food Stress or Hunger +Female Contribution +Latitude +Interaction
Female Status +Female Contribution +Latitude +Mean Stature
Female Status
Food Stress or Hunger

3.5.3. Statistical Software

All regression modelling performed for this study was calculated using STATA 14, as was the polychoric principle component analysis (Kolenikov and Angeles, 2009) used to compose the female social status variable. Some incidental and summary statistical calculations used SPSSv24. Various charts presented throughout this thesis were generated using either STATA, SPSS, or Excel. The map of society locations (Figure 3.1) was generated using Google fusion tables (Google 2016).

3.6. Methodological Limitations

In order that the hypothesis, methods, results, and conclusions of this work can be properly assessed, it is important to acknowledge and discuss potential limitations within the data and procedures relied upon. Whilst I addressed general methodological concerns (those associated with the use of comparative methods) in Section 2.1, limitations inherent to the methods of this particular study are discussed in detail here.

At least two possible sources of error arise due to the use of the Standard Cross-Cultural Sample (or any other cross-cultural database): one of these is inherent to the sample itself, the other relates to its application. Firstly, information coded within this database has been compiled from multiple ethnographic studies conducted across different cultures, in varying geographic locations, and at different periods in history. This diversity of sources creates significant potential for variation in ethnographic sampling methods, and thereby compounds any potential for sampling error. Having said this, we can be reasonably confident that the published accounts included within the sample have been carefully and repeatedly peer reviewed, and were statistically coded by experienced and highly regarded experts in cross-cultural analysis (i.e. Murdock and White, 1969).

A second area of potential error in using any similar cultural database comes from the interpretation I have placed upon each of the variables selected for use (Section 3.4). Given that the ethnographic realities of each cultural group were observed and statistically coded independently from my own study, there exists the potential for misinterpretation of a given variable and its specific implications. In the absence of first-hand ethnographic experience of each society included in the sample, I can only assume that my considered interpretation of a listed variable is an accurate indication of real world social realities.

Specific aspects of the morphological data used for this investigation may also provide a source for error, and three particular issues are highlighted here: One is the difference between sampling dates for cultural information in the Standard Cross-Cultural Sample and stature data I collected for each group. Although the ethnographic information was collected for periods of cultural independence (pre-industrialisation and pre-European colonisation), some stature measurements were made much later. Since the method employed for this study relies upon correlations between cultural variables and morphology (mean male and female stature), the fact that sample times for stature may be several decades removed from the point of cultural sampling introduces potential for misrepresentation of cultural effects. I minimised these differences, wherever possible, by selecting stature data collected from as close as possible to the focal sampling date listed in the Standard Cross-Cultural Sample.

A second data issue relates to my use of stature estimates calculated from long bone measurements for some groups (i.e. for the ancient Romans and pre-Columbian Aztecs). This introduces a potential for error in at least two possible ways. The first issue is that the appropriate conversion factor for calculations of stature from long bone measurements is known to vary between populations and it is difficult to predict the appropriate conversion factor for past groups. The second concern is that expected differences in size between the sexes are often used to apportion sex to skeletal remains. This introduces a level of potential for circularity in determining stature sexual dimorphism from this material. In regard to both of these issues, I must assume that the professional researchers providing these data points (Henneberg and Henneberg, 2002; Comas (1949) cited in Newman 1962) were familiar with these error potentials, and that sample sizes and conversion factors were appropriate to ensure adequate scientific rigor.

The third area of potential statistical error within this study arises due to the limited number of cases where both stature and cultural data were available. Of the 92 cultural societies coded for stature sexual dimorphism, only 28 had all of the required cultural information to allow their inclusion in the final regression models. This was due to the limited number of societies with data coded for the combination of 'female social status' and 'food stress or hunger'. Although this number of cases is considered adequate for the present study, future research should seek to expand the stature sample or use alternate cultural variables allowing more societies to be included in regression analysis.

Finally, because of time constraints inherent to Advanced Masters-level research, I only used one potential indicator of relative self-domestication—that is, the level of mean size sexual dimorphism. I selected this variable on the basis that it is considered an effective morphological indicator of domestication within Neolithic remains of butchered mammals (Helmer et al., 2002; Zeder, 2008, 2012). However, future investigations may be improved by incorporating more of the documented traits associated with domestication syndrome (Table 2.2).

Chapter 4:

Results

4.1. Descriptive Statistics

4.1.1. Dependent Variable

Mean male stature was significantly higher than mean female stature for all 92 societies included in this study. Figure 4.1 shows the correlations between male and female stature results from across the sample. The linear trend of this data (solid line) has an R^2 value of 0.933. The dashed diagonal line designates the position of theoretical stature equality—where male and female stature are the same (i.e. the sexual dimorphism ratio is 100%). Although there is inter-societal variation in male and female stature, and in sexual dimorphism, all societies in my sample were above the line of stature equality. In other words, in all of the societies, mean male stature is higher than mean female stature and sexual dimorphism is greater than 100%.

Mean stature sexual dimorphism for the sample of 92 populations included in this analysis was 107.5 (SD=1.1). This result is consistent with previous assessments of mean stature sexual dimorphism for human populations (Ralls, 1976; Gaulin and Boster, 1992). The highest score was 110.0 for the Aztecs of central Mexico. The lowest was 104.7 for the Haida people of western Canada. This represents a range of 5.3 difference in stature sexual dimorphism across these societies.

4.1.2. Independent Variables: Predictors and Controls

In Table 4.1, I provide summary statistics for all of the variables. The sample size for each variable indicates how many of the societies contained information for that

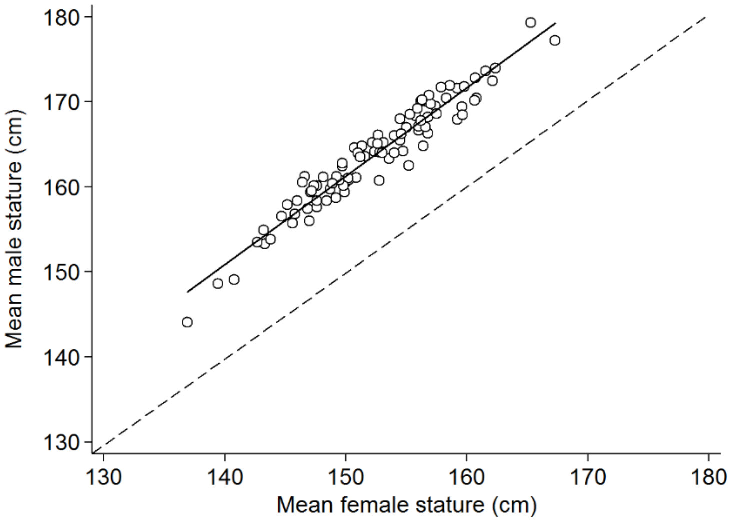

Figure 4.1. Scatterplot of mean male stature versus mean female stature (in cm) for each of the 92 societies. The hashed line is the theoretical line of stature equality. The solid line is the best-fitting ordinary linear regression line.

Table 4.1. Summary statistics for all independent variables.

Variable	n	%	M	SD	Min	Max
CONTINUOUS VARIABLES:						
Female status	37	--	-1.21	0.9	-2.4	0.7
Mean stature	92	--	158.1	6.0	140.5	172.3
Absolute latitude	92	--	24.9	18.8	0.3	68.7
% Female contribution to subsistence	50	--	4.6	1.5	1	8
CATEGORICAL VARIABLES:						
Food stress or hunger:						
Food constant	25	36	--	--	--	--
Occasional hunger or famine	31	44	--	--	--	--
Periodic or chronic hunger	14	20	--	--	--	--
Region:						
Africa	13	14	--	--	--	--
Circum-Mediterranean	14	15	--	--	--	--
East-Eurasia	24	26	--	--	--	--
Insular Pacific	11	12	--	--	--	--
North America	14	15	--	--	--	--
South America	16	17	--	--	--	--

variable (in the case of the first four, continuous, variables), or the number of groups that returned a positive result for that variable (in the case of the categorical variables: 'food stress or hunger' and 'region'). This is relevant because, in the subsequent multiple regression analyses, the number of observations differed from model to model because some variables had missing data.

4.2. Multivariate Analyses

4.2.1. Linear or Non-linear Covariates?

In Table 4.2, I provide the results of the AIC analysis which compared the model fit of linear and nonlinear (quadratic) forms for each of the continuous variables. Because 'food stress or hunger' was converted to dummy variables, checking for linear or non-linear fit was unnecessary for this variable. According to these results, the 'female social status' and 'proportion of female contribution to subsistence' variables showed a closer linear correlation to stature sexual dimorphism than non-linear. However, each of the other variables showed a stronger non-linear relationship. Graphical representations of simple bivariate regression between stature sexual dimorphism and each of the chosen variable forms (linear or nonlinear) for each of these four continuous variables are presented in Figure 4.2.

Table 4.2. AIC values for linear and nonlinear versions of the regressions. Check marks indicate the most well supported form of the covariate.

	Linear	**Nonlinear**
Female status	111.51 ✓	113.5
% Female Contribution to Subsistence	156.16 ✓	158.06
Absolute latitude	282.02	274.65 ✓
Mean stature	283.96	279.69 ✓

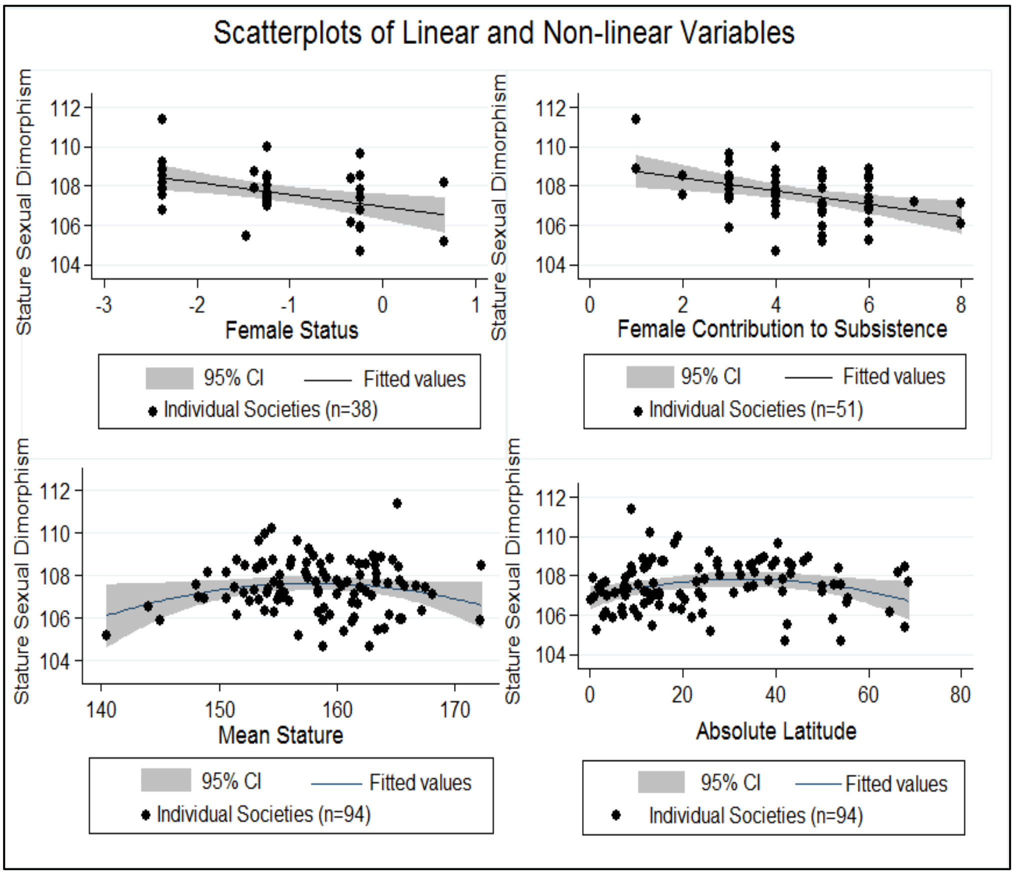

Figure 4.2. Fitted scatterplots of four linear and non-linear variables.

4.2.2. Multiple Linear Regression Models

In Table 4.3, I present the results of the AIC analysis of multivariate regression models. It shows AIC scores and ranking (based on ΔAIC) for each of the 25 candidate models. Model 1 had the lowest AIC score, but Model 2 had an AIC that was only slightly higher (ΔAIC=0.0003). All other models had ΔAIC of greater than 2, so only Model 1 and 2 were used for inference. I provide full details of the two multiple linear regression models used for inference in Table 4.4 (because, as stated previously, neither was sufficiently better fitting than the other based on AIC results). There were no notable differences in the estimates for coefficients included in both models—all were within 0.01 of each other—and both models had an R^2 of 0.677, but Model 1 included a term for '% female contribution to subsistence' while Model 2

Table 4.3. Ranked list of assessed regression models with AIC and ΔAIC scores.

Model	**Rank**	**AIC**	**ΔAIC**
Female Status +Food Stress or Hunger +Female Contribution +Latitude +Mean Stature +Interaction	1	65.94	-
Female Status +Food Stress or Hunger +Latitude +Mean Stature +Interaction	2	65.94	0.0003
Female Status +Food Stress or Hunger +Female Contribution +Mean Stature +Interaction	3	68.30	2.36
Female Status +Food Stress or Hunger +Mean Stature +Interaction	4	68.36	2.42
Female Status +Food Stress or Hunger +Female Contribution +Latitude +Interaction	5	70.83	4.89
Female Status +Food Stress or Hunger +Latitude +Interaction	6	71.07	5.13
Female Status +Food Stress or Hunger +Female Contribution +Interaction	7	72.07	6.13
Female Status +Food Stress or Hunger +Female Contribution +Latitude +Mean Stature	8	72.16	6.22
Female Status +Food Stress or Hunger +Interaction	9	72.25	6.31
Female Status +Food Stress or Hunger +Latitude +Mean Stature	10	72.76	6.82
Female Status +Food Stress or Hunger +Female Contribution +Mean Stature	11	75.88	9.94
Female Status +Food Stress or Hunger +Female Contribution +Latitude	12	75.89	9.95
Female Status +Food Stress or Hunger	13	75.96	10.02
Female Status +Food Stress or Hunger +Latitude	14	75.97	10.03
Female Status +Food Stress or Hunger +Mean Stature	15	76.22	10.28
Female Status +Food Stress or Hunger +Female Contribution	16	76.84	10.9
Female Status +Female Contribution +Latitude +Mean Stature	17	108.28	42.34
Female Status +Female Contribution +Mean Stature	18	110.46	44.52
Female Status +Latitude +Mean Stature	19	110.54	44.6
Female Status +Latitude	20	110.82	44.88
Female Status +Female Contribution	21	111.07	45.13
Female Status	22	111.51	45.57
Female Status +Female Contribution +Latitude	23	111.68	45.74
Female Status +Mean Stature	24	112.12	46.18
Food Stress or Hunger	25	212.69	146.75

Table 4.4. Details of the two multiple linear regression models used for inference.

	β	RSE	P	95% CI	
Model 1:					
Female social status	-1.175	0.143	0.000	-1.543	-0.807
Food stress or hunger:					
Food constant	--	--	--	--	--
Occasional hunger or famine	1.711	0.52	0.022	0.373	3.049
Periodic or chronic hunger	2.508	0.32	0.001	1.683	3.333
Interaction terms (status x hunger):					
Female status x 'Occasional hunger or famine'	0.936	0.214	0.007	0.385	1.486
Female status x 'Periodic or chronic hunger'	1.043	0.736	0.216	-0.849	2.937
% Female contribution to subsistence	-0.001	0.091	0.986	-0.232	0.236
Absolute latitude (nonlinear):					
Absolute latitude	-0.002	0.028	0.949	-0.07	0.074
Absolute latitude^2	-0.0002	0.0004	0.615	-0.001	0.0008
Mean stature (nonlinear):					
Mean stature	2.078	0.932	0.076	-0.319	4.476
Mean stature^2	-0.006	0.003	0.077	-0.013	0.001
Constant	-60.41	74.155	--	--	--
Model 2:					
Female social status	-1.174	0.141	0.000	-1.538	-0.81
Food stress or hunger:					
Food constant	--	--	--	--	--
Occasional hunger or famine	1.709	0.493	0.018	0.439	2.978
Periodic or chronic hunger	2.503	0.502	0.004	1.211	3.795
Interaction terms (status x hunger):					
Female status x 'Occasional hunger or famine'	0.934	0.235	0.011	0.328	1.54
Female status x 'Periodic or chronic hunger'	1.04	0.872	0.287	-1.2	3.28
Absolute latitude (nonlinear):					
Absolute latitude	-0.002	0.028	0.953	-0.072	0.075
Absolute latitude^2	-0.0002	0.0003	0.594	-0.001	0.0007
Mean stature (nonlinear):					
Mean stature	2.082	0.836	0.055	-0.067	4.231
Mean stature^2	-0.006	0.002	0.056	-0.013	0.0002
Constant	-60.685	66.444	--	--	--

Note: n=28 for both models. Model 1 was the most well-supported model (R^2=0.677). Model 2 was the second most well-supported model (R^2=0.677, ΔAIC=0.0003). Both models include robust standard errors to account for clustering on the 6 regions.

did not. Critically, as predicted, both of these superior models included terms for the interaction between the predictors of interest. In both models, the interaction term for 'female status x occasional hunger or famine' was significant but the term for 'female status x periodic or chronic hunger' was not. The interaction effects are shown in Figure 4.5, Panel A. They are based on estimates from the best-fitting model (Model 1) rather than using a multi-model average, which is justified since the coefficients in the best-two models are almost identical.

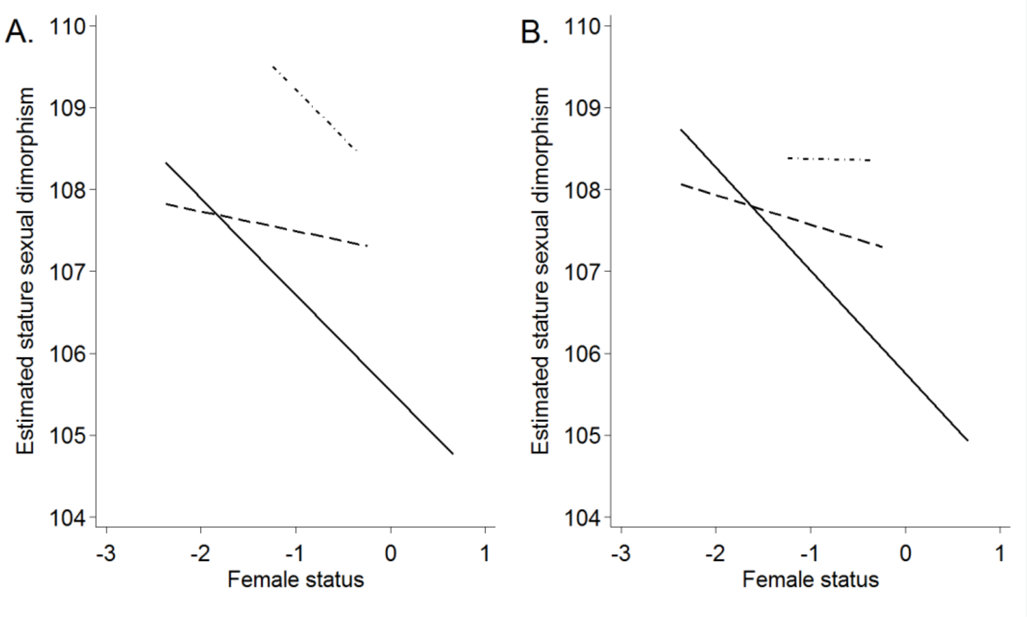

Figure 4.5. Relationship between female status and stature sexual dimorphism for three levels of food security: food constant (solid line), occasional hunger or famine (hashed line) and periodic or chronic hunger (dash-dot line). Panel A is based on estimates from the best-fitting multiple regression model; Panel B is based on three ordinary linear regression models, one for each category of food security.

As predicted and shown in Figure 4.5, Panel A, increased female social status is associated with lower stature sexual dimorphism, and the magnitude of this effect is conditioned by food security. Under conditions of no food stress (the reference category: 'food constant'), female social status has a significant negative effect upon stature sexual dimorphism. Furthermore, also as predicted, under conditions of occasional famine or hunger, the magnitude of the effect of female status is somewhat lessened—indicated by the relatively more horizontal trend line. However, in the most drastic category of food stress or hunger, ‘periodic or chronic hunger’, higher female social status is associated with lower sexual dimorphism, as predicted; but, contrary to prediction, the effect appears as strong as it is when there is no food stress.

At least two possibilities exist for the final, contrarian, result. On one hand, the interaction between female social status and food security may be nonlinear. Female status may have a larger effect on stature sexual dimorphism in the lowest and highest categories of food security and a smaller effect in the middle category, as the model suggests. On the other hand, this result could also be an artefact of the model and the small number of data points in the third category of food security. In fact, the available data support this second possibility. Cross-tabulation of the raw data (Table 4.5) shows decreasing food security does have a linear gradient effect on the relationship between female status and stature sexual dimorphism. Further, the series of ordinary regression models shown in Figure 4.5, Panel B, also support this possibility.

Table 4.5. Comparison of mean stature sexual dimorphism for high and low female status across the three categories of 'food stress or hunger'.

Food Stress or Hunger	**Female Social Status**	***n***	**Mean Stature Sexual Dimorphism %**	***Diff. (%)***
Food constant	Low	4	107.71	
	High	5	105.86	1.85
Occasional hunger or famine	Low	11	107.93	
	High	3	107.26	0.67
Periodic or chronic hunger	Low	4	108.38	
	High	1	108.36	0.02

Note: ‘High’ and ‘low’ were calculated as above or below the mean female status score for the entire sample of 92 cultural groups (see Table 4.1, M= -1.21).

In order to contextualise the results of this analysis, Table 4.6 illustrates the distribution of societies considered in the final regression models according to categories of female social status and food stress or hunger. The mean stature sexual dimorphism for each of these categories is provided in parentheses for simple comparison.

Table 4.6. Categorisation of 28 societies based on high or low female social status and level of food stress or hunger (mean stature sexual dimorphism in parentheses).

		Food Stress or Hunger		
		Food Constant	**Occasional Hunger or Famine**	**Periodic or Chronic Hunger**
Female Social Status	**High**	Ashanti, Garo, Iban, Haida, Jivaro. (105.86)	Nama Hottentot, Semang, Comanche. (107.26)	Goajiro. (108.36)
	Low	Ibo, Toda, Javanese, Quiche. (107.71)	Kikuyu, Pastoral Fulani, Amhara, Egyptians, Irish, Kurd, Punjabi, Vietnamese, Alorese, Japanese, Chukchee. (107.93)	Gilyak, Montagnais, Papago, Aztec. (108.38)

Note: As for Table 4.5, 'high' and 'low' female social status was calculated as above or below the mean female status score (-1.21) for the entire sample of 92 cultural groups.

Chapter 5:

Discussion

5.1. Effects of Female Social Status and Food Security

The results of my analyses provide strong support for the hypothesis that female status and food security interact in shaping stature sexual dimorphism. Higher female social status is associated with less sexual dimorphism, and the effect is stronger when food is relatively more secure. In the category of lowest food security, ‘periodic or chronic hunger’, this apparent trend reverses, but further analyses suggest that this is an artefact of a small sample size of societies in that category. These effects are consistent with the expectation that under worse environmental conditions, where nutritional resources are relatively constrained, women will tend to prefer more-masculine male mating partners (Brooks et al., 2010), which implies a higher degree of intersexual selection for masculinity and aggression.

Interestingly, the increasing trend in stature sexual dimorphism under food constraint is exactly opposite to that predicted by multiple previous authors (see Gray and Wolfe, 1980; Frayer and Wolpoff, 1985). According to these and other sources, sexually dimorphic physiological processes should mean that nutritional deficits will suppress male stature more significantly than female stature and should, therefore, lead to a decrease in stature sexual dimorphism within a given population. One explanation for the alternative result from this study is that an existing level of male-biased parental investment could be intensified under food insecure conditions. This would imply that where food availably is constrained, male children are preferentially fed, and girls are relatively more malnourished. If this is the case however, then all previous expectations of decreased sexual dimorphism in environments of poor nutrition have failed to account for the effect of cultural preferences in favour of male children—as have multiple scientific findings which supported these expectations (reviewed in Gray and Wolfe, 1980; Frayer and Wolpoff, 1985).

This male-biased parental investment explanation is similar, but opposite, to that proposed by Holden and Mace (1999) to account for diminished stature sexual dimorphism among groups with a high female contribution to subsistence. Notwithstanding that the present study found no significant influence from female contribution to subsistence, sex-biased nutritional investment must be considered as a potential explanation for the trends observed here. It is possible that variables used in this study to compose the indicator for female social status (Figure 3.2), could be associated with situations where parents preferentially feed girls due to the role they play in either inheriting property themselves, or in ensuring the familial transfer of wealth from male property owners to sister's sons, or other matrilineal heirs. In this case, it might be plausible that low stature sexual dimorphism could be caused by girls receiving biased nutrition under conditions of high female status, and that high dimorphism under nutritional stress could be caused by boys receiving a similar biased treatment.

However, these straightforward nutritional explanations for the results of the analyses are contradicted by the observed interaction effect between 'female social status' and 'food stress and hunger' (Figure 4.5, Panel A, and Table 4.5). This shows that high female social status had a greater effect upon stature sexual dimorphism in situations where food was constant, compared to environments where food was increasingly constrained. If parental investment biases were particularly influential, we might still expect that a decrease in nutritional security could lead to an increase in male stature (hence higher stature sexual dimorphism) where female status was low, but we would also expect a counter diminishment in dimorphism where high status girls should benefit from similar parental bias. Even if high female status did not promote nutritional bias towards girls under these conditions, we should still expect a lack of bias towards boys, which would at least maintain the relative levels of stature sexual dimorphism across all three categories of food availability. Instead however, it appears there is an increasing trend in stature sexual dimorphism under conditions of nutritional constraint, regardless of high or low female status.

Simple expectations of increased male and female height due to better nutritional conditions are somewhat undermined by the observation that, across the full sample of 92 groups, situations where the food supply was relatively secure (i.e. ‘food constant’) showed the lowest mean stature for both males and females, and females under periodic or chronic hunger showed the highest mean stature for their sex. Perhaps as a reflection of this latter observation, in accord with earlier findings by Eveleth (1975), the present study found that African populations were the least sexually dimorphic. Based on her results, Eveleth (1975) concluded that stature sexual dimorphism had a strong genetic component and, therefore, could not be taken as a useful indicator of nutritional status.

The effects of the predictors of interest considered here were not diminished after controlling for proportion of female contribution to subsistence, a potential confounder that was present in one of the two multiple regression models used for inference. This implies that the previously reported significance of this variable may have been the result of a capacity to confer elevated female social status, rather than an association with higher parental investment and improved nutrition in girls, as suggested by Holden and Mace (1999). It may be noted that high levels of female contribution to subsistence would imply a degree of female control over nutritional resources, which seems likely to predict for increased female social status.

This interpretation is supported by the findings of Alesina et al. (2016) which showed high social status for women in societies where female participation in subsistence activities is high. Such conditions can be contrasted with those found in situations where physical strength requirements (e.g. for big-game hunting, or plough-based agriculture) limit female participation in subsistence activity and predict for low female social status, including elevated levels of violence against women (Alesina et al., 2016). High female contribution to subsistence is also associated with high pair-bond instability due to female defection (Quinlan and Quinlan, 2007)—which may indicate high female social status, and is certainly suggestive of an elevated level of female mate choice.

5.2. Implications for Human Evolution

Evolutionary theory regarding divergent male and female mating strategies suggests males increase their reproductive output by securing multiple partners, whereas female reproduction can be optimised by inducing maximum paternal resource investment in support of partner and offspring (Bateman, 1948; Trivers, 1972). These two somewhat conflicting, but fundamental, mating strategies are likely to exert opposing influences with regard to average levels of masculine morphology and behaviour. Intrasexual selection (male-male competition) will tend to promote higher aggression and increased masculinity among males. This should be associated with taller male stature and increased stature sexual dimorphism within a population. Conversely, as indicated in this study, under certain conditions, intersexual selection (female mate choice) is likely to favour less aggressive and less competitive males who are more inclined to invest paternal resources towards mates and their offspring. This would effectively select against excessive masculinity and lead to decreased male stature and stature sexual dimorphism within a given population.

Puts (2010) provides a pertinent observation with regard to the relative influence of these two sexual selection mechanisms when he states that divergent selection pressures may interact in predictable ways, and may, at times, conform to a hierarchy of influence. For instance, where extreme intrasexual competition and male mate-guarding is in operation, effective exclusion of all potential competitors will entirely nullify the influence of other sexually selective forces—e.g. female choice, or sperm competition (Puts, 2010).

This insight is highly relevant to the current investigation because it implies that in societies where cultural norms significantly impede the free exercise of female choice (for instance, due to patriarchal marital arrangements, or by condoning sexual coercion and jealous mate-guarding behaviours), women's preferences are less likely to affect selective outcomes. It follows from this that social systems which privilege either male or female mating strategies will tend to drive average levels of stature sexual dimorphism, masculinity, reactive aggression, sociability, and cooperation in one direction or the other. As such, prevailing cultural norms form an important part of the socially-constructed niche (discussed by Sterelny, 2011, 2012) within which much of humanity's recent evolution has taken place.

For example, along with an overall trend towards increased 'feminisation' in human craniofacial evolution over the past 200,000 years, Cieri et al. (2014) also found recent agriculturalists had more masculine facial morphology (at least with regard to facial shape, if not brow ridge morphology), when compared to human foragers—both ancient and recent. In light of the findings of the present study, these observations may imply divergent levels of intersexual selection for lower aggression between hunter-gatherer and agriculturist groups. Previous studies have shown that hunter-gatherers tend towards relative egalitarianism (Cashdan, 1980; Woodburn, 1982; Dyble et al., 2015; but see Smith et al., 2010), whilst agricultural groups—

especially those using heavy ploughs, which lessen female contributions to subsistence—tend to be more hierarchical and male-dominated (Alesina et al. 2013; 2016). As such, female social status would be relatively higher in forager societies, and this would imply that female mate choice capacity should also be relatively increased. In addition, it has been shown that agricultural groups may be relatively less well-nourished and can experience more frequent famine than traditional hunter-gatherers (Nickens, 1976; Meiklejohn et al. 1984; Bentley et al., 1999; Berbesque et al. 2014). In accord with the findings of this present study, instability in food supply would predict that among agricultural societies even where women were able to exercise their own mate choice preferences, they would tend to prefer relatively masculine and competitive male partners who are more capable of monopolising constrained resources. These two inferred characteristics of recent agricultural groups (lower female social status and relatively worse nutritional conditions), may explain Cieri et al.'s (2014) observations of increased facial masculinity in these societies when compared to contemporary and earlier foragers—an effect which those authors do not discuss or explain in detail.

There is presently some debate within evolutionary anthropology in regard to which form of sexual selection (intra- or inter-) has been the most influential in male human evolution (Puts, 2010, 2016). Hill et al. (2017) claim that male contest competition is the most parsimonious explanation for a range of male traits which are apparently adapted for combat (including large size). These arguments are logical if current states of dimorphism are the only available evidence. However, incorporating past conditions allows assessment of overall morphological trends which may be more relevant to the evolution of humans as we know them today. It seems unlikely that male contest competition could explain both early hominin male adaptation for contest, as well as subsequent diminishment in traits associated with this contest, e.g.

declines in facial masculinity (Cieri et al., 2014) and male size reductions, leading to diminished human size sexual dimorphism (Frayer, 1980; Frayer and Wolpoff, 1985; Hill et al., 2017). The suggestion that these shifts result from the invention of hand-held weapons, whilst the intensity of male-male competition has remained constant through to the present day (Hill et al., 2017), fails to explain other lines of evidence for diminished aggression and competition in males over this period of hominin evolution.

A more parsimonious and compelling explanation for the suite of evolutionary changes that have occurred since the start of the Late Pleistocene, is a reduction in contest competition following sustained selection for lower reactive aggression—as occurs under domestication (Trut, 1999; Trut et al., 2001; Wilkins et al., 2014). Where intrasexual selection promotes a less masculine and less-aggressive average male, this might also lower the intensity of male intrasexual competition, hence creating further impetus towards self-domestication. It would follow, therefore, that levels of stature sexual dimorphism can imply more than simply whether male-male competition is relatively intense or not; among recent human societies at least, there exists a corresponding implication that female mate choice is correspondingly relatively influential.

Another alternative explanation for the numerous morphological trends described as evidence for human self-domestication is that they result from changes in hunting technology and ecological niche (Frayer, 1980; Holden, 1999; Ruff, 2002). This line of reasoning suggests that Late Pleistocene changes emerged due to an overall trend towards gracility affecting males more than females because of diminished selection associated with typically-male subsistence activity, especially big-game hunting.

However, unlike the human self-domestication hypothesis, the two alternative mechanisms mentioned above (the invention of weapons and changed hunting technology) do not identify positive selection in favour of size reductions—or any of the other noted traits associated with self-domestication (Groves, 1999; Leach, 2003; Cieri, Churchill, Franciscus, Tan, & Hare, 2014; Hare, 2016). Rather they rely upon the expectation that removal of previous selective pressure in favour of large size and robusticity would inevitably promote smaller size and gracility due to simple energy and growth efficiencies. Unfortunately, without further empirical exploration, it is hard to assess the relative influence of a tendency towards energy efficiency versus mechanisms of positive intersexual selection in favour of diminished masculinity and less reactive aggression.

In contrast to these alternatives, according to the hypothesis proposed by Cieri et al. (2014) the increasing sophistication and spread of multiple human technologies—including weapons—reflect sustained selection for diminished aggression and increased sociability, as do coincident morphological shifts occurring across this time. According to this line of thinking, without behavioural changes leading to increased social capacity, widespread and significant improvements in shared technological ability are unlikely to have ever occurred. This is not to suggest that all male contest competition ceased from the Late Pleistocene onwards—this is certainly not the case (see, for instance, Wilson & Daly, 1985). However, it does imply a diminishment in its influence as well as, perhaps, a shift in the relative importance of intrasexual and intersexual selection over this period.

The results of the present study provide significant support for the possibility of human self-domestication occurring via intrasexual selection. However, I have not attempted to test either of the alternative explanations for selection against aggression in humans: i.e. fitness improvements enjoyed by less-aggressive, more-sociable, individuals (Cieri et al., 2014), and collective ostracism of excessively-aggressive group members (Pinker, 2011; Wrangham, 2014). Given all three forms of selection could plausibly occur in any human society, it seems unlikely that only one of them would have driven selection against aggression in *Homo sapiens*. Within the complex social milieu of relatively modern humans it seems reasonable to expect that all three have operated simultaneously at various times.

Having said this however, as explanations for self-domestication leading to social cooperation and behavioural modernity, both of these suggested alternatives to intersexual selection do imply a certain circularity. This is because both of them inevitably assume a pre-existing level of sociability and group cohesion. There are sound logical reasons to expect that cooperative benefits and collective ostracism could not provide a cause for the level of sociability that they would require in order to operate in the first place. By contrast however, the logic of intrasexual selection represents a truly primal impetus, effectively operating since the emergence of sexual reproduction itself, and being particularly relevant to the reproductive success of female placental mammals due to the high parental investment this mode of reproduction entails (Trivers, 1972; Davies et al., 2012).

If we consider the differences between our nearest extant relatives, chimpanzees and bonobos, as a proxy indicator for the range of potential behaviours present in early hominins, it is apparent that group cohesiveness and collective action do not automatically entail lower aggression, or self-domestication, even among highly-derived primate species. Male chimpanzees within a given group will tend to be close kin and will periodically form cohesive bands for hunting and violent intergroup raiding (Furuichi, 2011; White et al., 2013; Gruber and Clay, 2016). They are also known to form within-group alliances which help to assert and maintain dominance hierarchies (Wrangham, 1986). Despite these socially coordinated activities however, chimpanzees have failed to self-select in favour of less behavioural aggression. In fact, male dominance and aggression continue to maximise individual reproductive success

(Wroblewski et al., 2009; White et al., 2013). Sexual coercion and sperm competition are also common among chimpanzees, and females tend to mate with multiple males in order to limit the likelihood of infanticide (Muller et al. 2009; Muller et al. 2010).

By contrast, whilst still being male philopatric, bonobos show much lower signs of aggression (Kano, 1992; Furuichi, 2011; White et al., 2013). This results from intersexual selection which has promoted a process of self-domestication and the traits of domestication syndrome within this species (Hare et al., 2012). The capacity for female bonobos to select against male aggression is a result of their relatively higher social status which occurs largely due to the presence of coalitionary bonds between females (Furuichi, 2011; White et al., 2013; Tokuyama and Furuichi, 2016). These bonds are, in turn, thought to result from the relative nutritional abundance of bonobo habitats (White, 1998).

Despite potential similarities, the prevalence and success of intersexual selection for lower aggression among bonobos does not (on its own) provide compelling evidence that the same process was involved in the self-domestication of humans. However, this comparison between the two species of *Pan*, does demonstrate that capacity for collective action in primates is not sufficient, by itself, to promote selection against aggression. Within hominin evolution, the intensity of group interaction may have fluctuated from time to time, making individual cooperative ability more-or-less beneficial, and collective ostracism more-or-less effective. However, the potential benefits for hominin females who were able to avoid sexual coercion and who began to procure supportive paternal investment, suggest that intersexual selection would have provided a persistent impetus towards self-domestication and the wider cooperative capacities this is likely to have promoted.

Future empirical studies may contribute to knowledge of human self-domestication by considering the relative influence of social benefits and collective ostracism in more detail. However, my present expectation is that intersexual selection is likely to provide the most foundational and consistent mode of selection against aggression since the alternatives could only begin to operate after a significant level of cooperation and social complexity had already been achieved by other means. The results of my current research suggest a strong association between female social status and relative levels of self-domestication among recent cultural groups. Although underlying sexual stature disparity may have occurred due to prehistoric male contest competition, recent variation suggests significant moderation as a result of intersexual selection and the reproductive logic of female mate choice decisions.

Chapter 6:

Conclusion

In this thesis, I have provided a convincing test of hypotheses related to the claim that human self-domestication can be driven by intersexual selection via female mate choice. My results support the prediction that societies where women have higher social status and secure access to nutritional resources will tend to show relatively elevated levels of human self-domestication—as indicated by lower stature sexual dimorphism. The analysis, which used multiple regression and multi-model inference, confirmed the expected interaction between the two predictors of interest. While there was some evidence for a non-linear interaction effect, the analyses suggest that this was an artefact of a model with a small sample size for one of the levels of food security.

Given the results presented here, it seems reasonable to conclude that intersexual selection against reactive aggression has contributed to apparent human self-domestication occurring from the Late Pleistocene onwards. This evolutionary process is demonstrated by changes in both facial morphology and stature sexual dimorphism, as well as other characteristics associated with domestication syndrome. Whilst underlying levels of sexual dimorphism may well result from contest competition between ancestral hominin males, more recent declines in dimorphism would imply a lessening in the selective influence of intrasexual competition. Although hominins undoubtedly began to acquire new weapons, changed prey species, and improved hunting technology over this period, these innovations cannot parsimoniously explain the wide range of traits associated with human self-domestication. However, we would expect this suite of characteristics to emerge under sustained selection against reactive aggression. This selection seems all the more likely given the apparent increase in human sociability and cooperation that precipitated our expanded cultural and shared technological capacities.

Future research on this topic would benefit from comparative examination of groups within a range of social and environmental conditions which might influence female capacity for mate choice, and relative preference for masculine male partners. In this regard, societies with matrilineal property inheritance are likely to provide especially useful data for further study. These investigations would also benefit by including more of the predicted morphological and behavioural indicators of domestication and human self-domestication within an expanded empirical analysis.

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Appendix 1:

Table of Stature Data for 92 Global Societies.

Society name	**Male stature**	**n**	**Female stature**	**n**	**Author/s (and listed society name)**
Nama Hottentot	162.4	73	149.7	27	Holden and Mace, 1999
Kung Bushmen	159.39	372	149.93	445	Holden and Mace, 1999
Nyakyusa	163.3	40	153.6	61	Hautvast, 1971
Hadza	160.5	36	150	31	Holden and Mace, 1999
Kikuyu	163.6	412	151.6	100	Holden and Mace, 1999
Ganda	166.6	322	156.04	308	Holden and Mace, 1999
Mbuti	144.05	579	136.91	414	Holden and Mace, 1999
Tiv	170.4	218	160.8	200	Kpela et al. 2016
Ibo	165.5	68	154.5	54	Holden and Mace, 1999
Fon	168.2	--	156.8	--	Cresta, 1971 (Dahomey)
Ashanti	164.21	48	154.74	27	Gustafsson and Lindenfors, 2009
Pastoral Fulani	173.92	74	162.37	71	Holden and Mace, 1999
Hausa	170.18	183	160.63	219	Gustafsson and Lindenfors, 2009
Massa (Masa)	172.8	24	160.7	50	Wiessner et al. 1998
Masai	166.94	450	155.03	513	Holden and Mace, 1999
Somali	179.3	204	165.3	215	de Lucia et al. 2002
Amhara	170	206	156.7	199	de Lucia et al. 2002
Kenuzi Nubians	169.5	127	157.4	282	Holden and Mace, 1999
Egyptians	171.6	--	159.2	--	Holden and Mace, 1999
Turks	165.2	39465	152.2	20263	Nevsi et al 2013
Romans	166	--	154	--	Henneberg and Henneberg, 2002
Basques	169.77	748	157.02	182	Gustafsson and Lindenfors, 2009
Irish	171.9	8902	158.6	1801	Gustafsson and Lindenfors, 2009
Lapps	164.1	240	152.4	248	Gustafsson and Lindenfors, 2009
Yurak Samoyed	160.1	--	147.6	--	Binford, 2001; Binford and Johnson, 2006; Kirby et al., 2016
Russians	171.8	--	159.8	--	Gustafsson and Lindenfors, 2009
Armenians	168	351	154.5	153	Kherumian, 1943
Kurd	166.1	598	152.7	31	Holden and Mace, 1999
Punjabi (West)	168.3	--	155.8	--	Holden and Mace, 1999
Gond	160.79		150.24		Pingle, 1984
Toda	170.79	213	156.88	112	Holden and Mace, 1999
Santal	160.5	197	149.8	213	Bose et al. 2006
Uttar Pradesh	164.6	--	150.7	--	Deaton, 2008

Society name	**Male stature**	**n**	**Female stature**	**n**	**Author/s (and listed society name)**
Khalka Mongols	164.83	59	151.33	49	Holden and Mace, 1999
Lepcha	161.12	130	148.16	112	Mukhopadhyay et al. 1996
Garo	160.7	--	152.79	100	Akhter et al. 2012; Jaswal, 2012
Vietnamese	157.6	--	147.6	--	Cresta, 1971
Khmer	161.05	365	150.84	75	Olivieret al. 1968
Siamese	168.56	200	157.48	200	Yodpijit et al. 2004 (Central Thai)
Semang	149.1	--	140.8	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016
Nicobarese	158.7	424	149.2	350	Sahani et al. 2010
Andamanese	148.58	163	139.43	156	Stock and Migliano, 2009 (Greater Andamanese)
Vedda	153.3	--	143.3	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016
Javanese	165.2	292	153.1	308	Hastuti, 2013
Iban	159.7	43	148.7	41	Gustafsson and Lindenfors, 2009
Alorese	158.39	846	147.6	149	Brouwer, 1935
Aranda	166.3	--	156.8	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016 (Northern Aranda)
Manus	164.05	75	152.82	98	Holden and Mace, 1999; Gustafsson and Lindenfors, 2009
New Ireland	161	946	150.2	61	Schlaginhaufen, 1964 (Neumecklenburg)
Mbau Fijians	172.45	146	162.15	151	Gustafsson and Lindenfors, 2009
Maori	173.6	124	161.56	98	Houghton, 2009
Western Samoans	170.4	101	158.3	144	Holden and Mace, 1999
Gilbertese	169.4	84	159.6	69	Furusawa et al., 2011 (Kiribati)
Atayal	160.1	96	149.8	147	Holden and Mace, 1999
Chinese	167.1	431	156	358	Gustafsson and Lindenfors, 2009
Manchu	157.4	168	146.84	141	Gustafsson and Lindenfors, 2009
Koreans	170.1	280	156.2	49	Holden and Mace, 1999
Japanese	158.39	171	146	91	Bennett and Hulse, 1982
Ainu	160.1	58	147.4	57	Chard, 1950
Gilyak	160.8	245	149.5	209	Chard, 1950
Yukaghir	156	--	147	--	Binford, 2001, Binford and Johnson, 2006, Kirby et al., 2016
Chukchee	165.08	70	152.64	82	Gustafsson and Lindenfors, 2009
Aleut	167.03	124	156.6	106	Justice et al. 2010
Copper Eskimo	164.8	82	156.4	42	Holden and Mace, 1999
Montagnais	166.2	41	154.6	29	Hallowell, 1929
Micmac	171.7	--	157.9	--	Hallowell, 1929 (Micmac and Abenaki)

Society name	**Male stature**	**n**	**Female stature**	**n**	**Author/s (and listed society name)**
Haida	162.5	--	155.2	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016
Yurok	164	--	153	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016
Yokuts (Lake)	164	--	151	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016 (Northern Valley Yokuts)
Paiute (North.)	168.55	--	155.29	--	Boas, cited in Sullivan, 1995
Klamath	168.47	--	159.65	--	Boas, cited in Sullivan, 1995
Comanche	167.8	--	156.2	--	Binford 2001, Binford and Johnson 2006, Kirby et al. 2016
Zuni	163.5	60	151.2	32	Holden and Mace, 1999
Papago	169.19	269	155.9	30	Holden and Mace, 1999; Faulhaber, 1970
Aztec	161.2	32	146.6	27	Comas, 1949, cited in Newman, 1962
Popoluca	160.5	103	146.4	100	Faulhaber, 1970
Quiche	153.8	117	143.8	83	Gustafsson and Lindenfors, 2009
Miskito	164	30	154	32	Holden and Mace, 1999
Cuna (Tule)	154.9	27	143.2	20	Steggerda, 1943
Goajiro	159.4	147	147.1	38	Stinson, 1990 (Guajiro)
Callinago	157.9	65	145.2	26	Neves et al. 1985 (Caribs)
Warrau	156.5	318	144.7	172	Stinson, 1990 (Worau)
Yanomamo	153.49	385	142.72	330	Holden and Mace, 1999; Gustafsson and Lindenfors 2009
Carib (Barama)	156.8	104	145.8	99	Holden and Mace, 1999
Cayapa	155.7	44	145.6	46	Stinson, 1990 (Chachi)
Jivaro	177.2	200	167.3	200	Meyers, 1937 (Jabaro)
Aymara	162.74	325	149.7	382	Holden and Mace, 1999
Shavante	170.2	42	156.3	39	Niswander et al. 1967 (Xavante)
Aweikoma	161.2	404	149.26	287	Neves et al. 1985 (Caingang)
Cayua	159.5	77	147.2	85	Stinson, 1990 (Caiua)
Mapuche	160.4	201	148.9	25	Stinson, 1990
Yahgan	158.36	382	148.43	258	Steggerda, 1943