A close-up, high-contrast photograph of a primate's face, likely a chimpanzee, with a focus on its large, expressive eyes and thick, textured fur. The lighting is dramatic, highlighting the texture of the hair and the intensity of the gaze.

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SAPIENT

The Undergraduate Journal of Biological Anthropology

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Spring 2022

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LETTER FROM THE EDITOR

Dear Reader,

The past school year has been yet another incredible feat in flexibility, accommodation, compassion, and readjustment. As students, community members, and individuals, we have all experienced both the joys and hardships of a return to in-person activities. Though tempered by the circumstances of the pandemic, we have had the incredible opportunity to reconnect with our campus and community—or to experience it for the very first time, along with all the excitement of a new place and new people.

I have been continually impressed by the resilience and dedication of the members of our journal. On behalf of the editorial board, I am thrilled to share the ninth volume of *Sapient*, Columbia's Undergraduate Journal of Biological Anthropology. This volume is packed full of articles that span the wide array of bioanthropological topics; the authors this year have written some most interesting and important papers I have had the pleasure of reading.

Having first joined *Sapient* as solely an illustrator, I am touched by the works of art we are fortunate enough to include in this volume. I hope that the efforts and talent of our illustrators are appreciated and that readers feel the impact of this art. My last year with *Sapient* has been a complete joy; I will cherish the opportunity I had to expand our editorial board, connect with new members, and see the passion and unique skillset each person brought to our journal. I am honored to have been this year's Editor-in-Chief, and to have been able to help foster the growth of our journal over the past three years. Looking to the future, I have nothing but excitement and high expectations for the new directions in which *Sapient* will travel.

To those reading, thank you for making all of our efforts worthwhile. I hope that you receive as much joy and inspiration from reading this volume as we did from creating it.

Aeja Rosette
Editor-in-Chief

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Illustration by: Astrid Jervis

The Black Death and Structural Violence in Late Medieval Europe

Laura Sibö Wang, *Washington University in St. Louis*

INTRODUCTION

Structural violence, a concept first proposed by sociologist Johan Galtung, describes “social structures that suppress agency and prevent individuals, groups, and societies from reaching their social, economic, and biological potential” (Haagen, 2012, p.31). This subtle form of violence, deeply rooted in social structures that have persisted over generations, influences the ability to access adequate nutrition, healthcare, and many other living conditions needed for maintaining health or survival; despite this, it has often been normalized and sometimes even completely overlooked (Haagen, 2012).

The COVID-19 pandemic exacerbates inequalities in our societies, and does not impact on everyone in the same way (Abrams and Szeffler, 2020; Tai *et al.*, 202; Williamson *et al.*, 2020). Multiple studies have found that racial and ethnic minorities are being disproportionately affected by the pandemic due to a variety of factors—including but not limited to preexisting chronic disease, housing insecurity, limited access to healthcare, and systemic racism (Abrams and Szeffler, 2020; Tai *et al.*, 2021; Williamson *et al.*, 2020). The inequalities that exist in our social structures directly cause the disproportional effects we observe not just during our present pandemic, but also during periods of significant distress in the past (Godde *et al.*, 2020; Haagen, 2012; Tai *et al.*, 2021).

Such disparities in health outcomes caused by structural violence can often be identified on the skeleton. Stressors in the sociocultural environment can disrupt “biological homeostasis and produce observable patterns of increased morbidity, such as disease, disruption of growth, and pathological processes” (Haagen, 2012, p.33). Through examination of skeletal remains, bioarchaeological research on structural violence sheds light on the lives of those whose voices were stifled and might have never been heard. In pandemics where inequalities are exacerbated, it is possible that more distinct patterns of biological stress can be detected in the remains of subordinate individuals or groups.

The Black Death is considered by some historians to be “the greatest natural disaster in the history of humankind” (Aberth, 2021, p.1). It is estimated that 63-75% of Europe’s inhabitants were infected, and 50-60% of the population were killed by the Black Death in the 1347-1353 outbreak (Aberth, 2021). The fatality of this historic outbreak, which occurred before the development of antibiotics in the 20th century, is estimated to be 80% (Aberth, 2021). Besides the Black Death, warfare and famine struck Europe during the Late Medieval Period (Cantor, 1994). The Black Death, along with the rest of the 14th century, therefore constitute a complex yet fascinating subject for bioarchaeological research. Focusing on the 1347-1353 outbreak, this paper examines and compares four London burial sites of the Late Medieval Period for potential indications of structural violence, the results of which may inform our understanding of other periods of distress, including our current COVID-19 pandemic.

BACKGROUND

Susceptibility to *Yersinia pestis*

Yersinia pestis, the bacterium now known as the cause of the Black Death and other plagues, spread in cities throughout Mediterranean Europe in late 1347 (Aberth, 2021). At this time, Europe had already been struggling with famine, with 1346-1347 considered to be one of the worst years in France, and 1340-1350 one of the worst decades in England (Carpentier, 1962). Intense urbanization was also occurring in major European countries and cities, which contributed to heavy environmental pollution and landscape change (Walter and DeWitte, 2017). Furthermore, 1347 was approximately a decade into the Hundred Years War, and conflicts between England and France were frequent (Byrne, 2012).

Therefore, when the plague struck Europe, its populations were likely not in their most prosperous and resilient conditions. Based on paleodemographic examinations of death assemblages at London cemeteries dating back to the 11th-13th centuries,

DeWitte (2015) observed a reduction in survivorship and increase in adult mortality in 13th-century populations in comparison to those from the 11th and 12th centuries, suggesting an overall decline in health that might have made late medieval populations particularly susceptible to the Black Death. This prediction of heightened susceptibility is consistent with genomic analysis of various *Y. pestis* strains; samples extracted from dental pulps of Black Death victims indicate no phenotypic evidence for increased virulence of the *Y. pestis* strain during this Black Death outbreak (Bos *et al.*, 2011).

Paleodemography of Plague Death Assemblages

The death rate of 14th century Europe was unsurprisingly high, due to the variety of disastrous events occurring simultaneously (Aberth, 2021; Byrne, 2012; Carpentier, 1962). It is therefore critical to distinguish how various disasters affected the human population differently. The concepts of catastrophic and attritional death assemblage describe whether a disaster, or disease in the current case, is indiscriminate based on the paleodemography of deaths (Aberth, 2021; Gowland and Chamberlain, 2005). Catastrophic assemblage, in which no particular age or sex sectors of the population was targeted, is categorized as indiscriminate; attritional assemblage, in which certain ages or sex sectors were targeted, is categorized as discriminate (Aberth, 2021; Gowland and Chamberlain, 2005). As summarized by Margerison and Knüsel (2002), war victims are usually an attritional assemblage of young adult males with high trauma rates; famine generally has more significant impact on people of young or old age, which is similar to natural attrition; massacre often demonstrates high trauma rates across all age groups and sexes, unless a particular population is targeted, hence a catastrophic mortality.

Debates surround whether plague discriminated among people in medieval Europe. A review of medieval plague pits by Bramanti *et al.* (2018, p.8) finds there to be a lack of evidence for “general trends of association between biological features.” Research by Signoli *et al.* (2002) indicates that the 1720-1721 *Y. pestis* plague in Martigues was indiscriminate, through a comparison of the age-at-death distribution for the plague and the distributions for the 1709-1710 famine and normal

mortality from 1702-1719. The 1720-1721 plague was caused by the same bacterium as the 1347-1353 Black Death outbreak, and the characteristics of its death assemblage may be generalizable to the earlier outbreak (Aberth, 2021; Signoli *et al.*, 2002). As illustrated in Figure 1, however, considerable variations in sex ratio and age distribution across sites should be recognized.

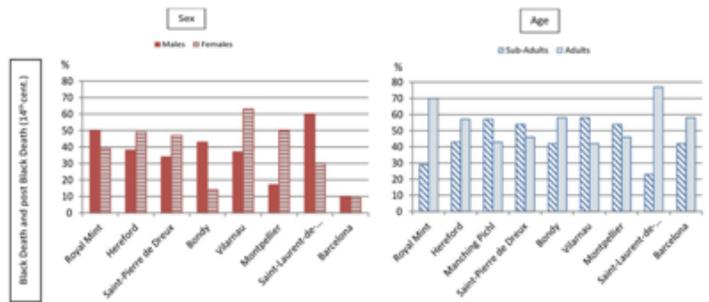


Fig. 1. Histograms of the sex (male/female) and age (sub-adult/adult) distributions of multiple plague pits used in the 14th century (modified from Bramanti *et al.*, 2018).

Skeletal Biomarkers on Plague Victims

Although there is no visible skeletal marker caused by *Y. pestis* infections, some critical biomarkers associated with developmental stress, metabolic disorders, and/or infections are extensively noted across plague victims from diverse sites and historical periods (Bramanti *et al.*, 2018). In medieval London, high frequency of enamel hypoplasia (EH) has been associated with famine burials in 12-16th century samples from St. Mary Spital Cemetery, and high frequency of periosteal lesions — the result of bone surface infection — is associated with attritional burial type (Yaussy *et al.*, 2016).

Enamel hypoplasia (EH) is one of the most common non-specific indicators of stress for bioarchaeology research, also frequently observed stress marker in reviewed studies, as shown in Table 1 (Bramanti *et al.*, 2018; Roberts and Manchester, 2005). EH occurs only during the development of dentition, presenting itself on the enamel surface as linear lines or grooves that persist into adulthood and remain detectable postmortem (Roberts and Manchester, 2005).

Diet, socio-economic status, and age-at-death have all been correlated with enamel hypoplasia, but the

exact cause and mechanisms remain unclear, with the main theory being childhood malnutrition (Bramanti *et al.*, 2018; Roberts and Manchester, 2005). Other pathologies of dentition, such as periodontitis and caries, have complex mechanisms of causation and are less clearly connected to specific populations or historical periods (Roberts and Manchester, 2005).

Table 1. Frequency of biomarkers of stress in adult victims of plague from different archaeological sites, periods and latitudes^a

Site	Period	Latitude	Sample (sexed adults)	Sex ratio	Freq. of Hypoplasia	Freq. of Cribra Orbitalia	Freq. of Hyperostosis
St. Pierre de Dreux	14 th c.	48.737112	26	0.73	56.2	31.3	17.6
Barcelona	14 th c.	41.386527	13	1.17	44.4	11.1	9.1
Royal Mint	1348-49	51.50267	377	1.26	75.5	18.3	90.0
Hereford	14 th c.	52.055908	92	0.77	89.0	13.0	33.3
Les Fedons	16 th c.	43.655419	56	1.15	76.4	20.0	
Maria Troon	16 th c.	51.025078	38	1.11	75.0	36.0	24.1
Puy St. Pierre	1629-30	44.53332	16	1.00	5.9		

^a Modified from Bramanti *et al.* (2018).

Periostitis, another indicator of poor health, presents as bony proliferation induced by inflammation (Roberts and Manchester, 2005). Since bone formation takes time, presence of periosteal lesions could reflect resilience and survivorship through stress (DeWitte, 2014; Roberts and Manchester, 2005). Osteoarthritis, usually associated with old age, could likewise Cribra orbitalia (CO) is also widely seen in plague burials. The cause of CO has been associated with iron deficiency due to “excessive blood loss through injury, menstruation [or] chronic disease such as cancer [or] parasitic infection of the gut” or an iron-deficient diet (Roberts and Manchester, 2005, p. 228). On the contrary, diffuse idiopathic skeletal hyperostosis (DISH), is not caused by any deficiencies, but rather a combination of rich diet and lack of exercise that are often associated with more affluent groups in historic populations (Roberts and Manchester, 2005).

Nutrition and Diet in Late Medieval England

Historic documents as well as the more novel method of isotope analysis have been used to study past diets, which complement the biomarker approach by obtaining further understanding of the physiological effects of structural violence on populations (Haagen, 2012; Müldner and Richards, 2006). In a recent study on

diachronic diet changes in pre- and post-Black Death adults from the medieval Berlin cemetery Petriplatz, Zechini *et al.* (2021) found a significant increase in nitrogen isotope values in post-Black Death skeletons compared to pre-Black Death skeletons, suggesting an increased consumption of animal protein; they found no statistically significant difference between males and females. This increase in animal protein consumption parallels conclusions drawn from historical records that demonstrate highly restricted access to meat and dairy products before the Black Death due to the limited amount of livestock disproportionate to the human population (Woolgar, 2006). Documentary sources such as tax and household records—along with isotope analyses of skeletal remains—also indicate drastic differences in diet between people of high status and those of lower status in medieval England (Müldner and Richards, 2006; Woolgar, 2006). These differences appear to have become more subtle after the Black Death (Woolgar, 2006).

A variety of factors are involved in determining the pre-plague frailty of individuals and the survivorship of individuals during the plague outbreak. Structural violence present in medieval societies likely inhibited lower socioeconomic groups from accessing much needed nutritional resources during the first few decades of the 14th century, and would likely have left a large number of the population especially vulnerable to the 1347-53 outbreak (Yaussy *et al.*, 2016). Famine may have had a significant and direct impact on the Black Death population, because of its critical contribution to conditions like childhood malnutrition which is manifested as high frequency of LEH in death assemblages (Bramanti *et al.*, 2018; Roberts and Manchester, 2005). Paleodemography studies suggested that the Black Death mortality profile differs from that of famine, and thus late medieval populations could have experienced or responded to famine and plague differently (Gowland and Chamberlain, 2005; Margerison and Knüsel, 2002).

This pilot study will explore pathologies present in remains from four London burial sites in use during the Late Medieval Period in order to identify potential biomarkers reflective of structural violence during the 1347-1353 outbreak of the Black Death.

CASE STUDY

Burial Sites

Data on burial sites used in this case study are from the Wellcome Osteological Research Database (WORD) by Museum of London. Among the numerous sites in use during the waves of plague across Europe, the Royal Mint (RM) located in London, England is particularly informative for an investigation of the Black Death and the specific 1347-1353 outbreak. The Royal Mint, also known as the East Smithfield Black Death Cemetery or later the Churchyard of the Holy Trinity, was an emergency burial ground established in 1349 by the clerk John Corey in direct response to the Black Death, and was exclusively used during the 1347-1353 plague (Byrne, 2012; Gowland and Chamberlain, 2005; Grainger and Hawkins, 1988; Hawkins, 1990).

It is estimated that around 2400 individuals were buried in the cemetery, roughly 6-15% of the approximated total deaths in London, and 3-5% of the city's population at the time (Byrne, 2012; Gowland and Chamberlain, 2005; Hawkins, 1990). The purpose of constructing an emergency burial ground was to deal with high death rates that had been overwhelming the existing cemeteries, and to allow quick yet appropriate disposal of bodies to control spread as well as to rest the souls of the dead in peace (Margerison and Knüsel, 2002). Therefore, bodies from geographically-convenient communities probably constituted much of the assemblage, including individuals of diverse age sex, and socioeconomic status (Grainger and Hawkins, 1988; Margerison and Knüsel, 2002). The overall preservation of remains is good, apart from the incompleteness of skeletons especially in subadults; a total number of 636 individuals were analyzed and recorded (Museum of London).

Since the Royal Mint was intended to be employed exclusively as the burial ground for Black Death victims during 1349-50, it offers researchers one of the best opportunities to study the effects of this plague. Age-at-death estimates were made by looking at the pubic symphysis and the auricular surface for adults, following the Suchey-Brooks criteria (Gowland and Chamberlain, 2005; Margerison and Knüsel, 2002). Assessments were also made with the levels of epiphyseal fusion and dental development for both subadults and adults (Margerison and Knüsel, 2002).

Closely related to the Royal Mint in terms of both site and population is the St. Mary Graces Abbey and Churchyard (SMG). In 1350, when the peak of the outbreak had already passed for London, the construction of the Abbey was granted by the King and initiated in the largely unused area of East Smithfield Cemetery (Grainger and Hawkins, 1988; Hawkins, 1990). St. Mary Graces was completed by late 1390s and was in use until 1538, having become one of the richest Cistercian Abbeys in England despite its small size (Grainger and Hawkins, 1988; Museum of London). Burials within the church include that of Sir Simon Burley, one of the most influential men then in the King's court; intramural burials appear to suggest higher social standing in contrast to graveyard ones (Grainger and Hawkins, 1988; Museum of London). Preservation and completeness of remains are comparatively poor, but 389 individuals in total were analyzed and recorded into WORD (Museum of London).

Other sites such as Spital Square (SS) and Merton Priory (MP) also offer insights into late medieval London, which may be generalizable to England or Europe at large. The Spital Square site was where the Augustinian priory and hospital of St. Mary Spital, one of the largest in medieval England, was located, and has burials from the 12th-16th centuries (DeWitte, 2014; Museum of London). Pathologies observed in the assemblage reflect a "typical medieval pathological pattern with high numbers of trauma and infection" (Museum of London). The Merton Priory site has 676 individuals—both monastic and lay—recorded in WORD, covering the entire period of monastic occupation from the 12th -16th centuries (Museum of London).

Methods

To measure the impact of structural violence in bioarchaeology, Haagen (2012) proposed two approaches: one is direct examination of differences in pathological rates between groups of different statuses; the other is analysis of diachronic health outcomes in historic contexts. It is difficult to rely fully on either approach in the current case of the Black Death in late medieval Europe because of limited accessible data and contextual information about all relevant plague pits. Therefore, both approaches are utilized in this study to complement each other.

Paleodemographic and pathological records from WORD were examined for the four aforementioned burial sites. Distributions of age-at-death and sex were used to determine whether the mortality profile of the Black Death population is attritional or catastrophic, as per Gowland and Chamberlain (2005) and Margerison and Knüsel (2002). Pathology rates were used to assess frailty, survivorship and environmental conditions, such as access to food or healthcare for different late medieval populations, following DeWitte and Bekvalac (2010), Godde *et al.* (2020), and Yaussy and DeWitte (2018). Paleodemographic and pathological findings were qualitatively compared both cross-sectionally and longitudinally. Comparisons of the former were made between death assemblages of distinct socioeconomic statuses; those of the latter analyzed assemblages from periods preceding, during and following the Black Death.

Findings

Mortality Profile

Based on age-at-death estimates of the Royal Mint assemblage using both the pubic symphysis and the auricular surface, the adult population's age-at-death distribution strongly resembles that of catastrophic mortality, which suggests that the Black Death equally affected all age groups and both sexes of the late medieval population in London, which may be generalizable to all of Europe (Gowland and Chamberlain, 2005). Similar conclusions have been drawn from primary assessments of epiphyseal fusion and dental development in subadults and adults (Margerison and Knüsel, 2002). More recent statistical work by Godde *et al.* (2020) also found neither age nor sex to significantly contribute to an individual's susceptibility to be infected and killed by the Black Death. These results confirm what medieval chroniclers describe as plague "striking down 'men of every condition, age and sex'" (Aberth, 2021, p. 5).

Yet, it should be noted that the sex ratio during the Medieval Period appears skewed, as documentary and archaeological records on medieval burial sites show consistently greater proportions of adult males (Bardsley, 2014; Byrne, 2012). An overall male to female ratio of around 2:1 is observed at the Royal Mint, St. Mary

Graces and Spital Square; at Merton Priory, where the population consists of monastic and lay individuals, over 90% are male (Byrne, 2012; Museum of London).

Pathology Rates

Although some samples with pathologies have been removed from the WORD East Smithfield collection, leading to underrepresentation of pathologies in the current available database, pathology rates maintain their analytical value (Godde *et al.*, 2020). The most prevalent skeletal pathologies in the Royal Mint (RM) population are CO (10.2% left, 9.4% right), and non-specific periostitis (11.8%) (Museum of London). Notable dental pathologies include caries and periodontitis, which were both present in 60.8% of all adults (caries = 63.1% male, 65.7% female; periodontitis = 62.5% male, 64.3% female), and LEH with a rate of 78.8% for adults and 35.2% for subadults (Museum of London).

In comparison to the St. Mary Graces (SMG) assemblage that chronically succeeds the Royal Mint population, the RM Black Death rates are higher for periodontitis (SMG = 64.5% male, 31.7% female), CO (SMG = 7.2% left, 7.7% right) and LEH (SMG = 53.1% adults, 21.1% subadults); but lower for caries (SMG = 68.8% male, 53.7% female) and periostitis (SMG = 15%) (Museum of London). A drop in both periodontitis and caries rates in female adults should be noted: in the case of periodontitis, 64.3% at the RM site to 31.7% at SMG, while their male counterparts experienced a slight raise from 62.5% to 64.5% (Museum of London).

According to available data on the Spital Square (SS) site remains in WORD, which primarily covers the 13th century preceding the Black Death but ranges from the 12th to 14th centuries, 16% of the overall population had non-specific periostitis; CO was prevalent (15% left, 12% right), and had almost double these rates in subadults; periodontitis was extremely common (90% male, 87.5% female), but caries were less so (50% male, 50% female); LEH was present in about 65% of adults and subadults (Museum of London).

At the Merton Priory site (MP), the majority of common pathology rates are not drastically different from those at RM, SMG or SS (MP adult LEH = 69.5%; CO = 11.5% left, 10.7% right; periodontitis = 80.1%; caries = 49.9%), but the periostitis rate at MP is much

greater, with an overall rate of 29.4% (Museum of London). In addition, pathologies little seen among assemblages at other medieval cemeteries in English had high rates within the MP population over the course of the 12th-16th centuries (Museum of London).

Osteoarthritis was found in 14.3% of the sample, the number being 5%, 1.7%, 4.9% in SS, RM, and SMG populations respectively; the rate for diffuse idiopathic skeletal hyperostosis (DISH) was 4.4%, doubling the rates for SS (2%) and SMG (1.8%), almost fifteen times greater than the rate for Black Death victims (0.3%) (Museum of London).

DISCUSSION

The mortality profile of the Black Death during the years of 1349-50 in London, England is indiscriminate across age groups and sexes (Aberth, 2021; Gowland and Chamberlain, 2005; Margerison and Knüsel, 2002). Because there has not been any significant mutation found in the strains of *Y. Pestis* that could potentially modify its virulence, the catastrophic profile seems generalizable to plague outbreaks at varied locations and during diverse periods of time in history (Bos *et al.*, 2011). Noted disparities in the number of individuals of different sexes at burial sites are not accounted for in this indiscriminate characterization of Black Death mortality; the male to female ratio is approximately 2:1 at three out of four sites of interest in this case study (Byrne, 2012; Museum of London). The skewed sex ratio is believed to be an exacerbation of pre-existing disproportions in medieval European populations, rather than selective mortality of famine or plague (Godde *et al.*, 2020). Because sex ratio at birth is around 1:1, and sex ratio at death is largely estimated among adults, the disproportionate sex ratio at death indicates an excess of female subadult deaths relative to male subadult deaths (Bardsley 2014). This disproportionality, existing in the presence and absence of disasters, could be caused by a combination of factors including less access to nutritional resources, the dangers of childbirth, and the burden of household chores, among other factors (Bardsley 2014; Godde *et al.*, 2020). The imbalanced sex ratio observed in Black Death assemblages thus confirms the presence and continuance of structural inequalities for women throughout the Late Medieval Period, despite

urbanization that created more work opportunities for women, and frequent warfare that would have required women to take up more dominant roles in households while men left to fight (Bardsley 2014; Godde *et al.*, 2020; Walter and DeWitte, 2017).

Statistical models involving pathology-based frailty index have shown that Black Death victims experienced more development-based pathologies than those who did not die of the plague (Godde *et al.*, 2020). LEH, one of the most common stress biomarkers, varies in frequency across assemblages of medieval cemeteries in London, England (Museum of London). According to WORD data, RM Black Death individuals exhibit LEH most frequently, with lower rates for both the SS population preceding the Black Death and the succeeding SMG population. The differences between LEH frequencies in males and females are smallest among RM Black Death victims, which could imply that the degree of early life stress was similarly experienced for both sexes among the majority of plague victims. The overall adult LEH rate at the MP site, known to have buried a larger proportion of high-social-standing individuals like the monastic population, is comparable to other sites (Museum of London). This lack of drastic difference in LEH rate among populations of varied socioeconomic statuses does not necessarily mean that socioeconomic status did not contribute to survivorship in medieval Europe, but it does suggest the possibility that living conditions and resources were far from ideal for all individuals during the 12th-16th centuries. Studies on late medieval diets support such a possibility, as examination of historical and archaeological records draw the conclusions that consumption of meat—a food type of greater nutritional value—was constrained by the limited number of livestock, and that dietary differentiations were rather subtle in medieval England (Müldner and Richards, 2006; Woolgar, 2006). Cribra orbitalia (CO), closely tied to iron deficiency, is also widely seen in medieval populations, with a frequency decreasing as the years progress among the SS, RM and SMG sites (Museum of London). The rate at MP falls within the range of the trend, again indicating the absence of disparity (Museum of London). As with the case of LEH, CO rates may be largely explained by the indiscriminate lack of sufficient nutritional resources for all groups in medieval English society.

Periostitis is most frequently present in the MP population, almost triple the rate in RM Black Death victims (Museum of London). Black Death-specific studies have shown an increase in age-at-death with higher rate of periosteal lesions, supporting periostitis as a biomarker for survivorship and longevity (DeWitte, 2014). Osteoarthritis, another pathology associated with old age, is also most frequently found at MP (Museum of London). The high frequency of periostitis and osteoarthritis in MP assemblage is unsurprising, as MP burials consist of larger proportions of monastic population who were of higher socioeconomic status, and likely had access to more resources to survive periods of significant distress in the Late Medieval Period (Museum of London). The discrepancies among the four sites of interest are similar for periostitis and osteoarthritis (Museum of London); the numbers suggest that Black Death victims were the least likely to survive, possibly with the shortest average lifespan, which is consistent with results from previous studies (DeWitte, 2014; Godde *et al.*, 2020).

Other diet-related pathologies further shed light on health differences due to social standing. Diffuse idiopathic skeletal hyperostosis (DISH) occurs more frequently at MP than the three other sites, likely due to the monastic/other high-status populations found there (Museum of London; Roberts and Manchester, 2005). Dental pathologies are somewhat difficult to interpret on their own, given the complicated mechanisms of causation, but evidence on nutrition and diet may help clarify current findings. Pre-Black Death SS and RM Black Death populations have comparable rates of caries and periodontitis for male and female adults. An evident drop in both periodontitis and caries rates in female adults is observed post-Black Death; in the case of periodontitis, 64.3% in the RM Black Death assemblage decreased to 31.7% in post-Black Death SMG, while their male counterparts experienced a slight raise from 62.5% to 64.5% (Museum of London). Periodontal disease can be attributed to aging, poor oral hygiene, protein and/or sucrose-rich diets that facilitate faster accumulation of calculus; caries are most prevalent in populations with high consumption of refined flour and fermentable carbohydrates in medieval Europe (Roberts and Manchester, 2005). The similarity in etiology for these dental pathologies could signify comorbidity and

address why similar changes are present in the two conditions. The rate drops in female adults may be due to their limited access to more refined or processed carbohydrates and proteins post-Black Death, in comparison to male adults, because of female inferiority in medieval Europe.

Structural violence towards women and the poor in late medieval Europe is not surprising. In this case study, the findings suggest that the Black Death acted differently on different types of inequalities. While sex-based inequalities were more subtle during the first half of the 14th century as the entire population was thrown into great distress, socioeconomic status-based inequalities were, more often than not, exacerbated by the disasters. Such aggravation is unsurprising, since individuals of lower social standing were likely already more compromised in health and had less if not minimal resources or opportunities to cope with famine, plague and war (Aberth, 2021).

Skeletal biomarkers have given us insights into how structural violence can impact human lives on a physiological level, and into how disasters can exacerbate structural violence in the past. Future quantitative analyses could confirm the findings of this case study, to investigate further the disproportionate sex ratios, to better account for potential confounding factors, and to test the generalizability of current findings to other outbreaks such as the COVID-19 pandemic. Admittedly, many questions about the Black Death, the Late Medieval Period, and structural violence remain unanswered, yet it is undeniable that bioarchaeology research can contribute to a better understanding of structural violence.

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Illustration by: Astrid Jervis

Do Non-Human Primates Have Culture?

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INTRODUCTION

The broadest definition of culture is the way that we do things (McGrew, 2004). Food, clothing, religion, law, gender norms, and much more fall under the realm of culture in humans. But do non-human primates have culture? If so, is it analogous or homologous to human culture? What might primate culture look like?

When it comes to non-human animals (from here on “animals”), settling on a single conception of culture becomes even more complicated than it already is. Some researchers reject the notion that non-humans can have culture outright (Galef and Laland, 2009). This calls into question what qualifies as human and whether our extinct relatives such as the Neanderthals and Denisovans should be included in such a description, but as there is little available discussion on this facet of the topic, this paper will focus on *Homo sapiens sapiens* (from here on “humans”) and the extant non-human primates (from here on “primates”). Some definitions of culture may emphasize exclusively human characteristics such as religion and law, but as such things obviously do not exist in the extant primates, this inherently precludes further discussion and cannot function as an operational definition for identifying culture more broadly (Hill, 2009; Kendal, 2008; Tennie and Tomasello, 2009).

For the purposes of this paper, I will focus on two broad ideas of animal culture and whether they have support in research surrounding primates. First, I will consider what I refer to as the “simple definition,” where culture is an array of behavioral variants that are inherited via social transmission rather than genetic transmission; here, social learning is the simplest and sometimes only criterion for determining if behavior is cultural in animals (Whiten, 2021). The meaning of culture does, however, become complicated as more criteria are added to the definition. I will thus move on to a more complicated viewpoint which I refer to as the “anthropocentric definition.” By this, I mean culture as referring to an emotional/moral aspect that is inherently tied up in personal and group identity, making it fundamentally about more than cultural *products* (such as

behaviors, objects, etc.) (McGrew, 1998; Tennie and Tomasello, 2009). This view would see such complex processes like ritual, signaling, symbolism, morality, group identity, and conformity as proof of *true* culture (Perry, 2009; Sterelny, 2009). From this viewpoint, one may also argue against primate culture on qualitative and/or quantitative grounds, i.e., that primate culture and the cognitive mechanisms behind it are not complex enough, and/or that primates do not have enough socially-learned behavior and/or behavioral variants to qualify as culture (Hill, 2009; Tennie and Tomasello, 2009).

This paper will examine examples of potential primate culture and attempt to evaluate whether they meet certain criteria, beginning with the simplest requirement of social-learning before searching for less certain criteria, such as imitation, teaching, cumulative cultural evolution, and conformity. I will also discuss criticisms of the arguments and methods of identifying culture. To conclude, I will state where I stand on this controversy and why.

SIMPLE DEFINITION: CULTURE COMES FROM SOCIAL LEARNING

Van de Waal and Bonnie (2009) argue that culture is applicable to any species where socially-transmitted behavior makes separate communities readily distinguishable. They put forth the simplest requirement for cultural behavior: behavior must be spread through social-learning rather than genetics or environment (Van de Waal and Bonnie, 2009). In the 1950s and 1960s, Japanese researchers observing Japanese macaques first reported the innovation of sweet potato washing amongst an isolated troop on Koshima Island; a female juvenile, Imo, was the original innovator, and her mother and juvenile peers were the first to follow (Van de Waal and Bonnie, 2009). The potato washing behavior appears to be the first documented primate innovation that went on to become a “tradition” (a group-specific behavior that comes from some form of social learning) (Van de Waal and Bonnie, 2009; Perry, 2009).

The simplest definition of animal culture does not require that culture be socially transmitted in a particular way (Van de Waal and Bonnie, 2009). One low-fidelity cognitive mechanism of social-learning is stimulus enhancement, wherein an observer witnesses a conspecific's focus on particular objects and begins to focus on them as well (Whiten, 2021). This mechanism requires only a common kind of associative learning, with the addition being that the individual learns from the perceived associations of another's behavior (Whiten, 2021). Local enhancement is a similar mechanism that draws attention to a particular location rather than an object, and the individual then learns on their own rather than from a conspecific (Laland and Janik, 2006; Whiten and van de Waal, 2018). Emulation is another form of social learning that is low-fidelity and common in primates, wherein an animal learns about the environmental *results* from another's actions (for example, that another chimp has a tool and has gained food via the use of that tool), but not the form of the actions themselves (Whiten and van de Waal, 2018). Traditions and cultural behavior can potentially be transmitted through such simple methods in both primates and humans, and I have seen no evidence that the existence of these mechanisms in primates is in debate (McGrew, 2015).

Cultural transmission may move vertically (information going from parent to child), horizontally (between conspecifics close in age), and obliquely (from one of an older age to a younger individual that is not their offspring) (Garland *et al.*, 2011). Whiten and van de Waal (2018) examined the role that social learning may play over the course of a primate's development. Social learning begins with primary caregivers—typically mothers—who serve as their offspring's first source of information about behaviors such as foraging, food processing, nest building, and grooming (Whiten and van de Waal, 2018). Then, as an animal approaches adulthood and their social circle expands, they shift to preferring other social models within their group (there is additional evidence that there may be biases in which models are preferred (Whiten and van de Waal, 2018). For example, Horner *et al.* (2010) concluded in one study that chimpanzees may be biased towards examining and learning from older individuals with high social status as opposed to younger individuals with lower status

(Whiten and van de Waal, 2018). Finally, at the age of adult dispersal, individuals come into social contact with new conspecifics and a new ecological environment, both of which they must learn about to survive (Whiten and van de Waal, 2018).

Since the initial discovery of sweet potato washing on Koshima, Whiten *et al.*'s (1999) landmark study established 39 behavioral variants that were 1) socially-transmitted, and 2) absent at some chimpanzee sites, but customary (occurring in most or all able-bodied members of one or more age-sex class) or habitual (repeatedly occurring in several individuals) in others, such that the tradition profile of each community was distinctly different from every other community. In this study, traditions varied widely from foraging behaviors to rain dancing and more (Whiten *et al.*, 1999).

Van Leeuwen *et al.*'s (2014) study reported on a group of chimpanzees at a sanctuary in Zambia where individuals began to spontaneously copy an arbitrary, non-adaptive behavior: sticking grass into their ear (grass-in-ear-behavior/GIEB, first observed in 2010). With a single and unrepeated exception in one group, GIEB was observed in only one of the four study groups and eight of twelve chimpanzees in this observed group repeatedly engaged in GIEB (van Leeuwen *et al.*, 2014). Almost all imitators of the behavior were shown simultaneously engaging in it with at least one other individual; in 61 of 65 of these occasions, an imitator was engaging in GIEB with the inventor, Julie, an adult female (van Leeuwen *et al.*, 2014). The first individual observed to engage with the behavior was Julie's son, Jack; the second individual to acquire it after him frequently associated with Julie, and the third and fourth individuals approached Julie more frequently than predicted by the group's average approach tendency (van Leeuwen *et al.*, 2014). Two individuals, one of whom was the fourth non-inventor to acquire the behavior, continued to engage in GIEB after Julie's death, though never doing so simultaneously while the study occurred (van Leeuwen *et al.*, 2014). The authors consider that the socially-learned aspect of the behavior, as well as its arbitrary nature, link it to human culture (van Leeuwen *et al.*, 2014), though interpretation of GIEB is limited by the small sample size.

An earlier paper observed group differences in grooming handclasp (GHC) behavior, where two

individuals groom each other with one arm each while lifting their other arms overhead and clasping each other's hands (van Leuwen *et al.*, 2012). They found that two of the four observed groups exhibited bouts of GHC, with marked differences in the style of GHC in each: the wrist-to-wrist style was significantly more frequent in group one, while the palm-to-palm style was significantly more frequent in group two (van Leuwen *et al.*, 2012). Arm length did not predict GHC style, and the behavior was a part of the behavioral repertoires for both groups for at least nine years and regularly spread to naïve individuals, with 20 of 23 juveniles from both groups beginning to partake in GHC behavior from 2010-2011 (van Leuwen *et al.*, 2012). More than 80% of the time, the initial partner of juveniles was their mother, supporting evidence for vertical transmission of behavior in chimps along maternal lines (van Leuwen *et al.*, 2012). These group differences were robust and consistent over time (van Leuwen *et al.*, 2012).

In the 1980s, a forest troop of wild anubis baboons lived near an open garbage pit from a tourist lodge (Sapolsky, 2006). Many of the most aggressive males in the troop foraged in the garbage pit in the morning; they had low engagement in male-female affiliative interactions (hence why they could visit the pit in the morning, foregoing the troop's morning socializing) and high engagement in dominance interactions (as competition in the pit with another troop was fierce) (Sapolsky, 2006). In 1983, infected meat from the garbage caused a tuberculosis outbreak, killing all of the males from the forest troop who ate there (46% of the troop's males) and changing the female to male ratio to 2:1 (Sapolsky, 2006). By 1986, this troop was unique for its relatively relaxed dominance, increased tolerance, and increased inter-sexual grooming (Sapolsky, 2006). By 1993, none of the adult males from 1986 remained, but the distinctive behavior of the group remained, adopted by the new males who had joined (Sapolsky, 2006).

These examples appear to meet the basic criterion of being socially-transmitted, and more are discussed in reviews, such as that of McGrew (2010) which examines chimpanzee technology, McGrew (2015) which discusses the origins of primatology and arguments for and against the concept of primate culture, McGrew (1998) which provides a broad overview of culture in primates, including some species

and genera not directly discussed in this paper, and Whiten (2021) which examines the reach of social learning across the animal kingdom.

For the purpose of considering if a behavior achieves the social-learning criteria, the most common tool is the method of exclusion (MoE, also known as the ethnographic method); a behavior is deemed cultural if it is present at a high level in some populations, but absent in others, and researchers can reasonably rule out ecological and genetic factors as a cause for this difference (Schuppli and van Schaik, 2019). The MoE is the basic tool that Whiten *et al.* (1999) used to identify cultural behavioral variants. Van Leeuwen *et al.* (2012, 2014) mentioned their use of this method to determine that transmission of GIEB and GHC behavior was socially-transmitted and thus, cultural.

The MoE does not lack problems. Social learning does not necessarily lead to population heterogeneity, leaving convergent culture (similarities in behavioral repertoires driven not by a common ancestral group, but by similar ecological conditions) and cultural universals (behaviors and knowledge that are consistently found across all populations of a species) unacknowledged (Schuppli and van Schaik, 2019). This also ignores behaviors whose variable forms are a response to ecological factors and resources, but are still socially learned (Schuppli and van Schaik, 2019). Thus, the MoE leads to biases in the types of supposed cultural variation that can be detected, favoring the social and technological domains over subsistence (Schuppli and van Schaik, 2019). Additionally, genetic differences do not themselves rule out social learning, and complex behavioral phenotypes are unlikely to be strictly learned versus innate (Schuppli and van Schaik, 2019). These factors, in addition to the fact that this method relies on geographic variation and thus how many populations can be compared to each other, means that the MoE on its own inevitably undercounts the actual number of potentially cultural traits (Schuppli and van Schaik, 2019). These issues are especially problematic because the MoE's criteria have become so ingrained that it has practically become a definition of culture itself rather than purely a tool, leading to cultural status being reserved for behaviors with geographic variation (Schuppli and van Schaik, 2019).

Sterelny (2009) adds that the MoE does not inherently show that individuals learn about their social environment in a distinctly social manner, and that while the inherent conservatism of this method is useful in identifying the capacity that a species has for traditions, it cannot on its own establish the *extent* to which a population depends upon traditions and social learning (Sterelny, 2009). Another problem is that it is logically impossible to exclude every potential ecological or genetic explanatory factor for a behavior, as some unknown variable could always be involved (Laland and Janik, 2006). Additionally, since culture is a way of creating adaptive behavior, correlations between behavior and ecology are to be expected; rigorous application of the MoE alone would thus exclude many potentially cultural traditions (Laland and Janik, 2006).

There are more criticisms of the research surrounding social learning in animals than those against the MoE. Classifying traits as either socially-learned or not is itself problematic given that phenotypic traits are always shaped by a combination of genetic and epigenetic dispositions, individual exploration, and social learning (Thornton and Clutton-Brock, 2011). Regarding interpretation, social learning is often assumed to result in homogenous within-group behavior even though this is not always the case (Thornton and Clutton-Brock, 2011). Additionally, individual cases of primate traditions always have the potential to be misinterpreted. One commonly debated example is ant-dipping, a behavior wherein a chimpanzee inserts a stick into an ant hill, withdraws the stick, and eats the ants that have become attached to the stick, with variation existing in stick choice and if the ants are removed by hand or mouth; researchers have proposed various social and ecological explanations have been suggested for variation in this behavior without broad agreement (Kendal, 2008; Tennie and Tomasello, 2009).

Finally, Perry (2009) adds more criticisms to methods of detecting social learning in primates. One method, mapping behavioral variation onto social networks to see which animals share which behaviors, does not actually illuminate the role of social learning in acquiring said behavior, or if it has a role at all (Perry, 2009). Experimental approaches are illuminating as they allow researchers to manipulate the subjects' environment and situation to their needs, but not all

species are easily manipulated and individuals often cannot be moved to new groups safely (Perry, 2009). Additionally, sometimes behavior that has been *trained* in an animal cannot be differentiated from actual cultural behavior, and results from experiments are not always meaningful to a species' natural state (Perry, 2009). Perry (2009) thus argues that observation of animals in their natural environment is critical, though not always possible.

Ultimately, there is not a satisfactory way to count traditions in primate species. The more that a primate population is studied, the more likely it is that researchers will discover diversity in both individual and group behavior, but not all species and populations can be given equal attention due to the simple reality that researchers do not have unlimited time and resources (Perry, 2009). Another problem with discussing the size of cultural repertoires is that there is a reliance on researchers' personal memories of studies, and different researchers use different methods as well as different levels of strictness (Perry, 2009). As such, problems may arise in how populations are compared and how these comparisons are interpreted.

In spite of these criticisms, it does not appear to be in doubt that many primate species learn via social transmission of information to varying extents, and that this learning happens via multiple cognitive mechanisms of various levels of fidelity and complexity (McGrew, 1998; Schuppli and van Schaik, 2019; Whiten and van de Waal, 2018). It is debatable to what extent different species do so, the number and complexity of traditions, which species are capable of higher-level cognitive mechanisms (if any), and how important traditions truly are in affecting behavior and fitness. Despite this, when we use the simplest criteria of culture in animals, many primates are cultural animals (McGrew, 1998; Whiten and van de Waal, 2018).

ANTHROPOCENTRIC DEFINITION: CULTURE AS IDENTITY

It may, however, be too reductive for social learning to be the sole criterion for culture. One way to differentiate human "culture" from animal behavior is quantitative; although there is currently no satisfactory method for accurately counting animal traditions, the repertoire size of human culture is generally taken to

greatly exceed anything known in any other animal (Perry, 2009). Chimpanzees have the largest known primate cultural repertoire, but no source puts *P. troglodytes* at even one hundred traditions (Whiten *et al.*, 1999). Therefore, if one's definition of culture is at least partially quantitative, no primate species would meet it.

That is not the only way to consider culture though; there are also qualitative factors in which this section will examine, as no primate species is likely to meet a quantitative definition. On one hand, there are cognitive mechanisms; human culture relies partially on novelty and invention (which some primates also possess) but also on high-fidelity transmission and the stabilization of existing traditions (Sterelny, 2009; Tennie and Tomasello, 2009). Certain cognitive mechanisms are believed to be both responsible and necessary for cumulative cultural evolution (CCE), such as imitation and teaching (Tennie and Tomasello, 2009). Imitation involves the copying of the exact form of another individual's actions and is assumed to be more cognitively complex and specialized than lower-fidelity mechanisms, such as emulation and stimulus enhancement (Whiten and van de Waal, 2018). Teaching, specifically active and intentional teaching, involves a teacher performing behavior at a cost to themselves to benefit the knowledge and development of a pupil (Whiten and van de Waal, 2018).

Certain researchers hold that human culture has an emotional quality to it that is not known to exist in animals (Hill, 2009; Perry, 2009). Ethnic markers are one way this quality manifests; ethnic markers are seemingly arbitrary behaviors and rituals performed by members of a particular group that serve both to strengthen social bonds and to advertise their group membership to those who exist outside of that group, allowing newcomers to identify potential enemies and allies (Perry, 2009). Ethnic markers tend to cluster with other traits such as sex, gender, subsistence techniques, etc., and coexist with social norms (Perry, 2009).

Social norms are standards of behavior based on shared beliefs about how members of a group should act; when someone acts outside of these norms, third-party observers with no personal stake may punish them for behaving "incorrectly" (Perry, 2009). Hill (2009) further adds two types of socially-transmitted information that he asserts exist only in humans: 1)

learned social regulations that shift the fitness costs of all aspect of behaviors (comparable to Perry's definition of norms) and 2) symbolic reinforcement of these regulations and elaborate displays to show that individuals follow a particular group and rule system (ethnic markers could be considered one form of this). These criteria of culture require a sense of conformity and group identity that has a moral, emotional element. But while it seems unlikely that culture as complex and elaborate as anything seen in *H. sapiens sapiens* exists in the extant primates, it may be possible that some species exhibit the foundations of these grander concepts. I will focus primarily on chimpanzees as the body of literature surrounding them is vast, and they are one of the closest relatives of humans, frequently considered to be more capable of higher cognitive mechanisms than many other primates. I will discuss other primates where relevant.

One concept considered vital to the complexity of human culture is cumulative cultural evolution (CCE), wherein innovation builds upon earlier inventions that have been incorporated into the existing culture, leading to a gradual accumulation of knowledge that allows current and future generations to benefit from and improve upon the inventions of the past (Tennie and Tomasello, 2009; Whiten and van de Waal, 2018). This process involves an accumulation of useful modifications, which requires process copying (wherein an animal copies the exact form of another's action) and is generally considered to depend upon high-fidelity mechanisms of social transmission of information, such as imitation and teaching (Kendal, 2008). To determine whether imitation and/or teaching exists or could exist in primates, I will examine both potential evidence for imitation and teaching and studies about CCE as it relates to primates.

Tennie and Tomasello (2009) hold that chimpanzees have neither imitation nor CCE, but rather that most chimpanzee "traditions" are behaviors that are easily inventable by multiple individuals and groups. They suggest that within-group spread of a behavior after it has been invented by one individual may be eased by low-fidelity mechanisms such as local enhancement and emulation, and that chimps are not capable of higher-fidelity social learning mechanisms (Tennie and Tomasello, 2009). There are, however, two points of possible contention that arise from their study: 1)

whether or not primates are capable of imitation and/or teaching, and 2) whether or not imitation is necessary for CCE in the first place.

The latter question has not been discussed to the same extent. Based on the results of their study, Caldwell and Millen (2009) suggest that CCE does not require imitation. Their study consisted of asking human participants to create paper planes in different conditions: some allowed for imitation (reproducing actions), some for emulation (reproducing results), and some for direct teaching (Caldwell and Millen, 2009). In each condition, 10 people would comprise a chain such that only one person was actively working on the paper plane at any time, and later participants had access to the planes that their group had completed previously (Caldwell and Millen, 2009). They found that all of the groups showed evidence of social learning and CCE, such that the final plane in each group was better than the previous planes, but no condition was overall better than any other (Caldwell and Millen, 2009). These results may be limited in part by the simplicity of the action and that it is non-adaptive. Unfortunately, there are few studies in the available literature that question whether imitation is necessary for CCE, although McGrew (1998) points to the Aka Pygmies (who learn many of the skills they use daily by either observation or practice) to show how culture may not depend on teaching.

Whether or not primates practice imitation and/or teaching is a contentious topic. McGrew (1998) cites several anecdotal pieces of evidence, such as chimpanzee mothers showing their young how to crack nuts properly and pigtail macaque mothers molding their offspring's locomotion. Boesch (1991) documented how chimpanzee mothers influence their offspring's learning about nut-cracking in three different ways. The first was by stimulating interest by leaving stones, intact nuts, and the infant near an anvil while the mother went gathering (which chimps without infants were not known to do) (Boesch, 1991). The second way of facilitating this behavior was providing good nuts and hammers, which infants on their own would have difficulty gaining access to, and which may come at a cost to the mother as she may now have to search for another for herself and may receive less nuts as a result (Boesch, 1991). The third way was actively teaching, where in two separate cases a mother observed her infant having technical difficulties

with nut-cracking, stopped their child, and demonstrated the correct way to do it (Boesch, 1991). In one of these cases, the mother was described as acting deliberately and slowly, though the motion itself was simple and would not take her long on her own; afterwards, the infant was more successful in the behavior (Boesch, 1991). These examples are potential evidence that chimpanzees practice imitation and active teaching, but not enough information has been collected to make a definitive conclusion.

Moving forward to other potential cases for CCE in primates, there is at least one archeological excavation that has unearthed chimpanzee technological remains (Mercader *et al.*, 2007). Mercader *et al.* (2007) discussed a Tai forest site in the Ivory Coast of Africa which appears to have been utilized by chimps. Modified stones—the unintentional by-products of bashing technology—found were dated to be 4,300 years old and were of a size, weight, and rock type (granitoid) that would be too large and heavy for percussive use by ancient humans, but are the exact type that extant chimpanzees tend to prefer (Mercader *et al.*, 2007). Starch residues found on the stones derived mainly from three nut species used exclusively by chimpanzees (Mercader *et al.*, 2007). The extrapolated behavior of these ancient chimps shows shared attributes with humans that indicate intelligence: the transport of material for projected use in another location, the optimal combination of material and size to perform an activity, and the creation of an activity area (Mercader *et al.*, 2007). Finally, they suggest that the nut-cracking behavior in the Tai forest chimps may have been transmitted over the course of hundreds of generations (Mercader *et al.*, 2007). If true, this suggests an ability for the faithful transmission of behavior that may allow this species to experience CCE, even if this particular behavior does not show signs of it.

One of the problems with establishing whether or not CCE exists in primates is that determining CCE requires having some idea of the original form of the behavior that has been built upon (Whiten and van de Waal, 2018). In humans, this is possible due to documentation (oral stories, artwork, written records, archaeological records, etc.) and the fact that in some cases, the original technology continues to exist in some form in certain cultures (Tennie and Tomasello, 2009).

In contrast, chimpanzee technology is often restricted to natural objects that degrade into the environment rather than being preserved, such as sticks, twigs, and blades of grass (McGrew, 2010; Whiten *et al.*, 1999). Another possibility—documenting the emergence of a new tradition and following it to see if changes accumulate—is difficult as researchers do not have unlimited time and resources to observe every population of a species, and every emergence of a new behavior, its progress, or lack thereof (Perry, 2009; Whiten and van de Waal, 2018).

Despite this limitation, documenting a new behavior can and has been done. Gruber *et al.* (2015) documented the spread of two novel behaviors in a group of wild chimps in Uganda: moss sponging and leaf-sponge reuse, both of which appeared in response to a context novel to the population. They suggest that the use of a new material (moss) in an old behavior (using leaves to sponge up water to drink) may show that chimpanzee traditions are not static, but rather that they gradually change over time and are more flexible than is generally thought, particularly in habitats that face degradation from human causes (Gruber *et al.*, 2015). For their study group in the Budongo Forest, Uganda, long-term behavioral records have established a baseline to which to compare new behaviors that emerge, illustrating how modifications to previous behavior can result in gradual change (Gruber *et al.*, 2015). Modifications may spread unevenly though, either due to biases in which behaviors are copied (such as the prestige effect, also demonstrated by Horner *et al.* (2010) and/or ecological conditions, which may be necessary to trigger certain innovations—such as the discovery of a new water hole in this case (Gruber *et al.*, 2015). Although only one possible example, this study by Gruber *et al.* (2015) suggests that chimps may be capable of modifying old behaviors to suit new environments and situations.

Regarding these examples, I would suggest that the case for CCE in primates is not as closed as some might believe. There are, however, two more related criteria for complex and human-like culture that I wish to examine: group identity and conformity. I define group identity as an emotional sense of belonging to a particular group of individuals. Conformity to certain group-determined behaviors, in this context, is a desire to behave like other members of one's group not only

for adaptive purposes, but rather due to an emotional desire to be similar and close to one's groupmates. I will now discuss potential evidence for such behaviors in primates.

Van de Waal *et al.*'s (2013) field experiment examined conformity of foraging choices in vervet monkeys. The researchers provided four groups of wild, but provisioned, vervets (totaling 109 individuals) with two trays of corn. In each group, one tray of corn was dyed pink, the other blue (van de Waal *et al.*, 2013). In two groups, the pink corn was altered to taste bitter without being harmful; the same was done to the blue corn in the remaining two groups (van de Waal *et al.*, 2013). In each group, the monkeys learned to avoid the bitter tasting corn, such that typically only low-ranking individuals occasionally ate it due to being unable to access the preferred corn (van de Waal *et al.*, 2013). Then, four to six months after originally provisioning the monkeys, the corn was provided again, still with pink and blue coloring, but now with the taste unaltered; over two months, each group maintained their original preference (van de Waal *et al.*, 2013). The researchers then examined the preferences of newcomers to the group, specifically, infants who were too young to eat the corn previously, and immigrating males (van de Waal *et al.*, 2013). They found that 26 of 27 naïve infants ate the locally preferred corn. The single infant who did not eat the locally preferred corn had a low-ranking mother who ate the nonpreferred food while high-ranking individuals monopolized the preferred corn, meaning all 27 infants followed their mother's preference (van de Waal *et al.*, 2013). Additionally, 10 immigrating males that came from groups who had a corn preference opposite to that of their new groups: seven of these males exhibited a first choice preference for the locally-preferred option (van de Waal *et al.*, 2013). When the males fed with no higher-ranking monkey nearby, nine of the 10 aligned with the local preference (van de Waal *et al.*, 2013). The single male who did not was unique in immediately taking the highest-ranking position in his new group (van de Waal *et al.*, 2013).

The authors suggest that their data show the importance social-learning has even at the expense of individual learning, particularly when it comes to food and foraging (van de Waal *et al.*, 2013). I further suggest that a conformity of behavior that overrides what one

previously knew to match the group—particularly regarding food, where a mismatch of knowledge could mean death—could show a tendency towards conformity that is analogous or homologous to that which exists in humans.

Within the Tai National Park, Luncz *et al.* (2012) observed that three neighboring chimpanzee groups (comprising a total of 45 chimps) showed different and consistent preferences for nut-cracking tools. In this environment, ecological conditions were similar for all three groups, and hardness of the *Coula edulis* nut decreases over the season for all of them (Luncz *et al.*, 2012). While chimps in the North and East groups gradually began to select wooden hammers towards the end of the season, the South group consistently preferred stone hammers; additionally, the East group had a steeper decline in proportion of stone hammers chosen over the season than did the North group (Luncz *et al.*, 2012). The original study found that, despite the fact that females typically immigrated into their adult groups, there was no significant difference between male and female hammer selection in any of the three groups (Luncz *et al.*, 2012).

Luncz and Boesch (2014) further investigated this lack of difference later on in a study examining the preferences of immigrant female chimps. Comparing both group and individual hammer selection behavior from 2008-2010, they found that in all three groups, there was no evidence of sex-based differences in hammer selection (Luncz and Boesch, 2014). Additionally, they tracked an individual female, Diva, who had newly immigrated to the South group at the beginning of the study period (Luncz and Boesch, 2014). They found that her behavior was significantly different between the two years of the study, with her behavior differing from the group's in the first year but progressively changing so that by the second year there was no significant difference between the two (Luncz and Boesch, 2014). As wooden tools are more abundant than stone tools in their environment, availability is not an issue, and the stone tools could potentially incur an additional energetic cost due to weight (Luncz and Boesch, 2014). The study supports the idea that uncertainty due to new circumstances and possibly intrasexual aggression directed towards new females could drive social conformity in these three

communities, but since only one female was this closely followed, it is not possible to make definitive statements (Luncz and Boesch, 2014).

Haun *et al.* (2012) and Whiten *et al.* (2005) conducted studies that further suggest conformity in chimps. Haun *et al.* (2012) used an experiment to investigate if their subjects (chimps, orangutans, and human children) acquired a strategy used by the majority of individuals or one demonstrated more frequently by a single individual. The observed action was dropping a ball into one of three colored boxes; each strategy was dropping the ball into a different box (Haun *et al.*, 2012). They found that seven of nine chimpanzees followed the strategy used infrequently by three individuals (the majority-biased response) rather than the strategy repeatedly used by one individual (Haun *et al.*, 2012). Human children also tended towards the majority response, but the orangutans' responses were randomly distributed (Haun *et al.*, 2012). They found that chimps considered the number of demonstrators more than the number of demonstrations when making a decision, while orangutans considered neither (Haun *et al.*, 2012).

An earlier study from Whiten *et al.* (2005) used a diffusion experiment to demonstrate a case of social transmission and possible conformity. In their experiment, researchers taught one individual in two separate groups of chimps one method of operating an apparatus to gain a treat (either “poke” or “lift”) (Whiten *et al.*, 2005). Afterwards, the other chimps in each group were allowed to observe their model at work before the task was made accessible to them (Whiten *et al.*, 2005). In each group, 15 of the 16 other chimps were successful in gaining a reward (Whiten *et al.*, 2005). All of the chimps in the “poke” group predominantly adopted the poking technique; in the “lift” group, however, the first six successful chimps predominantly adopted the lifting technique, but subsequent individuals were able to learn the poke technique on their own (Whiten *et al.*, 2005). Three chimps from the latter group learned and adopted both techniques, two more often used the lifting method, and four more chimps exclusively used the poke technique (Whiten *et al.*, 2005). When the apparatus was reintroduced after two months, they found that all but one user in the “poke” group used that method exclusively, and all but two in the “lift” group used the lifting method (the majority exclusively

so) (Whiten *et al.*, 2005). These studies by Haun *et al.* (2012) and Whiten *et al.* (2005) suggest that chimpanzees may have a tendency towards group conformity that is analogous and possibly even homologous to that of humans.

CONCLUSION

Ideas of how culture should be defined and what criteria should be considered for whether a species is cultural vary greatly (McGrew, 1998; Ramsey, 2013). The simplest criterion for culture is whether a species exhibits social transmission of behavior (Whiten, 2021). When additional criteria are demanded for a species to be considered “cultural,” it becomes more difficult to find primate species who can meet the definition. Though no living primate species has been observed to have anything approaching the complexity and size of human culture, there is evidence that some species may possess traits in common with human culture such as faithful transmission of behavior and group conformity that may result from a place of emotion (Perry, 2009; Tennie and Tomasello, 2009).

Since initially writing this paper, additional research has in fact been done, particularly documenting potential examples of cultural behavior in the extant primates. For example, this year (2022) there has been documentation of chimpanzees in Gabon using insects on open wounds as a form of self-medication and the medication of other group members (Pika, 2022). Other finds relating to chimpanzees concern whether or not they consider intent behind behavior, with recent experimental research suggesting they might do so in judging “wrongdoing” (Engelmann *et al.*, 2022). Another report hypothesizes that nut cracking may be a more complicated form of tool use, and an example of cumulative culture in some chimpanzee groups (Koops, 2022). Interestingly, other recent studies have focused on orangutans, with some evidence suggesting that they have individual artistic styles, that they know to use sharp tools to cut and hammer tools to strike without being taught, and that mothers may teach their offspring how to forage for food (Mikeliban *et al.*, 2021; Motes-Rodrigo *et al.*; Pelé *et al.*, 2021). Further research into these and other areas is still needed before conclusive statements can be made.

As more attention is given to searching for cultural behavior in primates, it is possible that evidence in favor of encultured primates will accumulate and more people will accept our similarity to non-human primates in this aspect. Even if such evidence does accumulate, the criteria may just become more demanding in response. The answer remains important due to the potential implications for human evolution, as well as the conservation of the living primates (Brakes *et al.*, 2021). Consider for example if chimpanzees were determined to have culture; conservationists would not only have to attempt to preserve individual animals and populations, but also any cultural traits they possess (Brakes *et al.*, 2021).

I am currently of the opinion that some species of primates, such as chimpanzees, possess a form of culture that is analogous to that of *H. sapiens sapiens*, if not directly homologous. This assessment stems from the evidence from such species as chimpanzees and vervet monkeys that group conformity may be similar/related to the emotional quality of group identity in humans. Additionally, much of the research in favor of animal culture is recent and more up to date than the opposite side, with evidence of primate traditions gradually accumulating. Ultimately, only time will tell if the dispute is ever resolved.

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Illustration by: Alex Prezeau

The Racial History and Problematic Present of the Body Mass Index

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INTRODUCTION

Tess Holliday, a beautiful, five-foot-three, plus-sized model graced the cover of *Cosmopolitan's* October 2018 issue; Piers Morgan (the rather infamous British broadcaster and media persona) publicly commented that this was “dangerous and misguided,” citing Britain’s battle with an “ever-worsening obesity crisis” (Baxter-Wright, 2018). After a recent February 2021 *Cosmopolitan* cover with the phrase “This is Healthy” featuring a plus-sized woman, Morgan again publicly voiced criticism, calling it “irresponsible” and citing a variety of health risks associated with obesity (Greep, 2021). While Piers Morgan was utterly immovable on the subject of obesity and poor health, the relationship between obesity and various aspects of health is complicated.

In a discussion of obesity, fatness, and health, an understanding of Body Mass Index (BMI)—currently used as a measure of fatness and determinant of obese status—is critical (Obesity and Overweight...updated 1 April 2021). Questions and debate remain about the true relationship between BMI, obesity and health. This paper will begin with the history and origin of BMI, cover the uses of BMI in the medical field with special emphasis on the “Obesity Epidemic” and Type 2 Diabetes, and conclude with current criticisms of and potential shortcomings of BMI. Given the importance of BMI’s historic and current relation to race/ethnicity, these connections will also be explored.

In any discussion involving populational affinity and/or ethnicity, word choice is important and carries meaning. I opt to use geographic ancestry terms (European/African/Asian) to maintain consistency; this terminology was applied throughout, including for studies that used color terminology (i.e., Black, White) for some/all of their subject groups. I do, however, retain the stated nationalities of research subjects if they are given rather than generalizing to a broader ancestry grouping. This complication of terminology is one

illustration that race, with its varying definitions and uses throughout time, is a complex subject (Hannaford, 1996; Marks, 2013; Smedley and Smedley, 2011). Most researchers currently define race a social construct, and not a biological category (Fuentes *et al.*, 2009; Gravlee, 2009); my use of the word race within this paper is rooted in that understanding.

ORIGINS OF THE BODY MASS INDEX

The origin of the BMI formula ($\text{weight}/\text{height}^2$) can be traced back to Adolphe Quetelet, a nineteenth century Belgian astronomer, mathematician, and statistician (Grue and Heiberg, 2006). He helped to pioneer the application of statistics to the human body, finding that the law of error—more commonly known as the normal distribution—applied to the variation within human characteristics (Grue and Heiberg, 2006). One characteristic of interest was weight, and Quetelet developed the Quetelet Index (W/H^2) to analyze weight in populations. Quetelet observed BMI of populations, not individuals, as he was primarily concerned with the average, which he viewed as a theoretical ideal from which all humans deviated. In his analysis of weight and other characteristics, he coined the term “l’homme moyen” (French for “the average man”), a concept expanded upon by Galton and other leading eugenicists (Grue and Heiberg, 2006). BMI can thus be traced back to the nineteenth century, though it was notably never intended by its creator for use in assessing individuals (Grue and Heiberg, 2006).

Despite its origin in the 1800s, the BMI formula was not the dominant method of determining weight status, nor was there a focus on obesity immediately following Quetelet’s development (Strings, 2019). Around the turn of the twentieth century, health insurance companies began to arise in the US; with business concerns at the forefront, they began to conduct large studies of mortality and create large data pools with information on populations’ weight, among

other characteristics (Strings, 2019). Medico-actuarial tables were created with different categories of weight, and their findings that excess weight could be correlated with higher mortality risk were also published (Strings, 2019). By the 1920s, these tables were gaining traction within the medical field, and alongside this was an observed increase in focus on excess weight, as evidenced by the marked rise in the use the words “overweight” “obesity” and “fatness” and decrease in those mentioning “thinness” or “underweight” in articles from the Journal of American Medical Association (Strings, 2019). Both doctors and their patients, who could be denied insurance or forced to pay higher rates, used these tables as their source of information on weight (Strings, 2019). Additional studies by insurance companies such as Metropolitan Life further emphasized the dangers of obesity, and even linked it to death, especially by heart disease and kidney failure (Rasmussen, 2019).

In the period before the wide circulation of the insurance tables, race and ethnicity were not important factors in the conversations about weight (Strings, 2019). Yet with the increasing impact of that data, the association of being overweight with disease, and doctors' rising concern over excess fat, racial and ethnic minorities became a factor in popular belief in regards to weight (Strings, 2019). Deemed inferior and more prone to excess weight/fatness, racial and ethnic minorities were seen as cause for concern and a threat to national health should they arrive in large numbers and intermix with the existing American population (Strings, 2019). This sentiment was especially targeted at Southern European and Jewish immigrants, though it was not scientifically supported (Strings, 2019). Concerns about weight were also connected to the eugenicist cause of strengthening the nation through the health of its white citizens in the name of achieving a “race of supermen,” published in renowned sources such as *JAMA* (Strings, 2019, p. 194). The focus of weight studies and concerns would remain on these middle-upper class white citizens, with hardly a single article published to *JAMA* about African Americans and fat in the early to mid-twentieth century (Strings, 2019).

It was in this period of increasing concern about and focus on weight that the term BMI would actually be coined by Ancel Keys, an American biologist and

physiologist (Strings, 2019). Keys had been personally off-put by the insurance tables and was a vocally criticized them for flaws he saw in their data/conclusions (Rasmussen, 2019). He also fought to change the definition of obesity from meaning excess weight to excess fat (Rasmussen, 2019). Keys was able to both work against the tables and achieve this second goal with the popularization of the use of BMI, which, once accepted, deemed the tables and conclusions made from their data nearly irrelevant (Rasmussen, 2019).

Keys *et al.* (1972) developed the term BMI and advocated for its increased use in the study “Indices of Relative Weight and Obesity.” In performing this study, Keys *et al.* (1972) aimed to find an easy, height and population independent index that could accurately assess an individual’s obesity (body fatness). To do this, he tested Quetelet’s index (W/H^2), the ponderal index ($H/W^{1/3}$), the simple W/H ratio, and relative weight (the percentage of the average weight of the population which was used by insurance companies) against independent, more accurate but less convenient, measures of body fat (Keys *et al.*, 1972). His subject groups were exclusively male and were drawn from populations in Minneapolis, Italy, Finland, Japan, and South Africa (Keys *et al.*, 1972). These populations were not necessarily representative of total populations, and Keys himself even states that the Batu men from South Africa were not representative of all Batu men in Cape Providence, let alone Batu men in general (Keys *et al.*, 1972). In regards to Quetelet’s Index (which he dubbed BMI), Keys ultimately said that “no more than half the total variance in body fatness is accounted [for] by the regression of fatness onto BMI” (Keys *et al.*, 1972). Despite these limitations, Keys concluded that BMI was as good an index as any of the others, and advocated for its usage on the basis of its simplicity of calculation, height independence, and population independence (Keys *et al.*, 1972).

SUBSEQUENT USES OF BMI

Soon after Keys introduced the term BMI, it would replace the medico-actuarial tables and would go on to have increasing use and impact in the medical and scientific communities (Strings, 2019). BMI has since played a critical role in major areas of health science, such as heart disease, diabetes, and more largely the

“Obesity Epidemic” (Strings, 2019). A mere 13 years after Keys coined the term BMI, it was used by the National Institute of Health in the publishing of their criteria for healthy weights (Strings, 2019). The World Health Organization (WHO) continues to use BMI to define overweight and obese, and lists high BMI as a risk factor for cardiovascular diseases, diabetes, musculoskeletal disorders, and certain cancers (Obesity and Overweight...[updated 1 April 2021]). Since its naming, BMI has continued to play a large role in health research and in the medical field as a whole. BMI can be found in published articles in connection to a wide range of topics, but this paper will elaborate on its relation to the ‘obesity epidemic’ and diabetes.

After medical scientists declared an ‘obesity epidemic’ in the 1990s, an array of different findings concerning BMI, obesity, and mortality were published (Rasmussen, 2019). In 2000, the Department of Health published “Healthy People 2010,” which included the goal of increasing the percentage of Americans within the normal BMI to 60% and reducing the percentage falling into the obese category to below 15% (Strings, 2019). Strings (2019) also states that the medical field encouraged Americans to take individual responsibility for their health and aimed to conduct more research on racial/ethnic minority health with the professed goal of closing the widening health gap between racial/ethnic minorities and European Americans.

Two especially notable studies with differing findings were those by Masters *et al.* (2013), the first to explore differences in obesity—decided by BMI—with regards to age, sex and race, and Flegal *et al.* (2013), a study that would engender heavy criticism (Strings, 2019). Masters *et al.* (2013) analyzed the National Health Interview Survey alongside the National Death Index from 1986-2006 for associations between obesity and mortality; they attributed 5% of deaths in adult men with African ancestry to overweight/obesity, 15.6% in men with European ancestry, 21.7% in women with European ancestry, and 26.8% in women with African ancestry. Overall, they declared obesity to be a much larger public health concern than previously believed, and encouraged public policy action (Masters *et al.*, 2013). These findings were in direct contrast to a study that found African Americans to have fewer years of life lost than European Americans at the same BMI

(Fontaine *et al.*, 2003). Another study by Flegal *et al.* (2013) also contradicted the findings of Masters *et al.* (2013); they found overweight to be associated with statistically significant lowered mortality, grade one obesity (BMI between 30 and 35kg/m²) to not be associated with increased mortality, and grades two and three of obesity (BMI between 35 and 40kg/m² and >40kg/m²) to be associated with higher all-cause mortality (Flegal *et al.*, 2013). Varying studies exist on obesity, BMI, mortality, and the ‘obesity epidemic;’ results are often contrasting and controversial, often heightened by fluctuating definitions of weight categories by BMI cut offs (Flegal *et al.*, 2013).

High BMI, as an indicator of excess fat, is currently regarded by the CDC as an important risk factor for diabetes (Diabetes risk factors...[updated 24 March 2021]). The majority of individuals with type two diabetes are classified as obese, and the increase in global prevalence of diabetes can be mostly accounted for by the global ‘obesity epidemic’ according to Eckel *et al.* (2011). Certain types of fat are closely associated with Type 2 diabetes mellitus (T2DM), such as upper body/visceral/ectopic fat (Bray *et al.*, 2018). In addition, the duration of high BMI is associated with an increased risk of developing T2DM, while weight loss is helpful in preventing the development of T2DM in pre-diabetics (Bray *et al.*, 2018).

SHORTCOMINGS AND CRITICISMS OF BMI

One central concern with BMI stems from its potential inaccuracies, especially when considering different ages, sexes, races/ethnicities, and degrees of musculature (McPherson, c2008). BMI still relies on a weight and height measurement, and is not an exact measurement of fat; it cannot distinguish between fat and lean tissue, nor can it determine the distribution and type of fat (Hsu *et al.*, 2015). Heavily muscled individuals, such as those that play competitive sports, will often have misleadingly high BMIs and it is advised that other methods of judging fatness be used (McPherson, c2008). Additionally, older individuals are found to have higher body fat than younger individuals with the same BMI, and women are found to have more body fat than men at the same BMI (McPherson, c2008).

Furthermore, as more studies have been conducted on non-European populations, more light has

been shed upon some of the ways in which BMI can be misleading and/or complicated. Several studies have found that Asians tend to have a higher percent body fat (PBF) than Europeans at the same given BMI (Pham *et al.*, 2019). The World Health Organization (WHO) reviewed such existing literature from 1990-2002 and released a statement that Asians have higher PBF than Europeans when holding age, BMI, and sex constant but did not release a new BMI cut-off point for obesity at the time (WHO, 2004). Some studies have found contrasting evidence; Pham *et al.* (2019) found that in Koreans over 60, men had similar PBF to Australian men and women had lower PBF than Australian women at the same age and BMI. It is worth noting that the Australian population was not strictly of European ancestry, but rather was considered representative of Australia's population (Pham *et al.*, 2019). Another study found a $24\text{kg}/\text{m}^2$ BMI to correlate to a PBF of 35% in both Vietnamese and European-American women (Ho-Pham *et al.*, 2010).

On the opposite end of the spectrum, African Americans have been found to have less percent body fat than European Americans at a given BMI (Rao *et al.*, 2015). In addition to overall percent body fat, another important health consideration that BMI is unable to account for is visceral adipose tissue (VAT), which may be a better indicator of metabolic risks (Carroll *et al.*, 2008). A study by Perry *et al.* (2000) found VAT to be significantly higher in European women than in African American women; they also found VAT to be a good predictor of health-related variables, though this relation depended mostly on European women and was not as strong in African American women. In agreement with previously published studies, Carroll *et al.* (2008) found African American men and women that were middle-aged or older to have lower VAT than Hispanic subjects and non-Hispanic European subjects at similar waist circumferences and BMIs. This study contributed to the emerging literature showing these differences in VAT by including Hispanics, men, and older aged individuals; most previous studies had been fairly small and in premenopausal women. The authors do, however, note that other studies have found African Americans to have the same or even higher VAT levels than their non-African counterparts (Carroll *et al.*, 2008).

Clearly many studies exist on the usefulness of BMI in different racial/ethnic groups, and contrasting findings abound. Authors also have differing opinions on how to best approach the problem of BMI, especially in regards to medical practice. In an article by Hsu *et al.* (2015), the authors advocate for a lowered obesity cut point of $23\text{kg}/\text{m}^2$ for diabetes screening in Asian Americans after an analysis of the literature covering Asian Americans' BMIs, body fat, and risk for type two diabetes (T2DM). They believe this lowering would increase Asian Americans' ability to be diagnosed with T2DM, receive education, and access preventative healthcare (Hsu *et al.*, 2015). In contrast, Cerdeña *et al.* (2020) advocate against adjusting BMI values by race in their article titled "From race-based to race-conscious medicine: How anti-racist uprisings call us to act." According to their findings, screening Asian patients for diabetes on the basis of lowered BMI cut points may increase their experience with stigma and/or their distrust of the medical field (Cerdeña *et al.*, 2020). The authors argue that medical professionals and clinical researchers should cease to "use race as a proxy for biological variables," and instead use more precise and accurate analytics along with a framework that recognizes that "racial health disparities are a consequence of structural racism" (Cerdeña *et al.*, 2020, p.1126-1127).

In regards to BMI and diabetes, one such analytic tool may be random plasma glucose (RPG). A study by Ziemer *et al.* (2008) found that RPG alone was a better predictor of glucose intolerance (which plays a large role in diabetes and pre-diabetes) than age, BMI, and race/ethnicity screening cut offs, and performed just as well as the continuous variable models. The authors recommend that RPG be further investigated as a screening tool for diabetes to aid in early preventative healthcare, as it is convenient and cost-effective (Ziemer *et al.*, 2008). Should RPG be further verified as a good screening mechanism, it may prove to be an effective way to avoid racial typology and adjustments of BMI in relation to diabetes.

Furthermore, there are important concerns about BMI and obesity in regards to anti-Black sentiment and the targeting of African-American women in particular. Noting terminology like the 'Obesity Epidemic,' Strings (2019) demonstrates how fatness has

been weaponized against women of African ancestry in particular as proof of disease. Women of African ancestry have historically been “symbols of ‘savagery’ aesthetic and amoral appetites,” and professing that they are disproportionately obese/ overweight using BMI as a new form of evidence simply adds a new veneer to such sentiments (Strings, 2019). Current anti-fat bias is not simply rooted in these newer medical findings, but rather existed previously and always carried with it a racialized element (Strings, 2019). Strong implicit and explicit anti-fat bias was found in medical doctors (along with the general public) in a large-scale study, though the results of these biases on overweight patients' healthcare was not detailed (Sabin *et al.*, 2012). As BMI is the primary tool used to define obesity/ overweight and measure fatness, such concerns about popular views of fatness clearly connect to the use of BMI. Critical analysis of the use and history of BMI and its relation to fatness and race remains important and unfinished work.

CONCLUSION

From its origin with Quetelet to its popularization by Keys, BMI has had a long history with the medical field, fatness, and populational affinity/race/ethnicity (Strings, 2019). Despite its current prevalence of use in screening for a variety of health conditions, debate continues over what information BMI can really provide about fatness and fat distribution, and what implications this has for different populations. Personally, I find that the slew of contrasting findings about BMI's predictive ability and accuracy—alongside its connections to volatile racial history and its enshrinement of biological racial categories—make BMI a troubling tool of the medical community and public at large. When considering the promise of RPG as a screening tool for T2DM, and the use of other more accurate measures of fat in many of the studies covered, I believe we should advocate for the continued effort to find new methods of assessing fatness and health that are both more accurate and do not subscribe to a typological race concept.

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Illustration by Priyanka Santiago

Unraveling deCODE: Genebanks, Research Ethics, and the Controversial Legacy of Icelandic DNA

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INTRODUCTION

In 1996, a team of American investors funded the biopharmaceutical company deCODE Genetics with the intention of analyzing variations in the genome of Icelanders and locating the genetic markers for common diseases (Gulcher and Steffánson, 2006). The creation of population genetics databases, colloquially known as genebanks, was ostensibly informed by scientific and economic motivations as well as ethical considerations. This essay argues that, while Iceland is purported to be an ideal sample group, it is difficult to determine an “ideal” homogenous population for identifying the genetic locations of common diseases. Moreover, the relationship between genebanks and both local participants and governmental health systems over the last two decades reveals the difficulty in balancing reliable data, participant consent, and the property rights of bioinformation for all parties involved. By examining the challenges faced by public and private ventures in population genomics projects this paper looks to bring clarity to the ethics of future research and legislation that navigate the emerging concept of genetic rights.

BACKGROUND

As the least densely populated country in Europe, Iceland has long received attention by scientists and historians alike for its insular geography and isolated heritage (Gulcher and Steffánson, 2006). After settlement by Nordic and Gaelic traders in the ninth century CE, the community largely retained its founding population of about 16,000 until 1850, after which it rapidly grew, culminating in its current size of roughly 360,000 (Ebenesersdóttir *et al.*, 2018). More recent examination of contemporary Y-chromosomes and mitochondrial DNA (mtDNA) suggests that the majority of matrilineal ancestry hails from Scotland, and about three-fourths of the patrilineal line can be attributed to Scandinavia, perhaps due to the hegemonic political influence of the Norse in the British-Irish Isles and the consequent introduction of Gaels to Iceland as

subservient members of gender-hierarchical society (Ebenesersdóttir *et al.*, 2018). Interestingly, Ebenesersdóttir *et al.* (2018) found that the mtDNA in the millennia-old Icelandic skeletal remains indicate a greater relationship with modern Scandinavians, Scottish, and Irish populations than with modern Icelanders. This distribution is likely caused by genetic drift resulting in a loss of mtDNA in the Icelandic gene pool (Ebenesersdóttir *et al.*, 2018). The study also analyzed differences in allele frequency using single-nucleotide polymorphism (SNP) arrays and concluded that the samples from ancient Icelanders are more closely related to contemporary Norse populations than to the modern Icelandic population, further suggesting genetic drift from an early founder effect (Ebenesersdóttir *et al.*, 2018).

Today, nearly two-thirds of Icelandic citizens reside in the capital city of Reykjavík where the sole tertiary healthcare facility, Landspítali (the National University Hospital), provides genetic health services, with an emphasis on cancer genetic counseling due to elevated population risk of breast and ovarian cancer (Stefansdóttir *et al.*, 2012). Icelandic healthcare infrastructure is designed to avail itself of centuries of medical records; citizens are therefore legally obligated to disclose any diagnosis of cancer to the national registry (Stefansdóttir *et al.*, 2012).

It is the country’s extensive recordkeeping and purported homogeneity that continues to pique the interest of researchers internationally (Gudbjartsson *et al.*, 2019; Gudmundsson *et al.*, 2019). According to historical records, a bottlenecking effect might be attributable to a 15th-century outbreak of bubonic plague, as well as a volcanic eruption in the 1700s, which increased genetic homogeneity (Marshall, 1997). This phenomenon was lauded by neurologist Kári Steffánson as more valuable than the wealth of genetic data from the demographically comparable Finnish population that was previously available (Marshall, 1997). With this potential in mind, Steffánson founded deCODE Genetics in 1996, with the intention of identifying the

genetic markers of common disease in Iceland's extensive genealogy with the same unifactorial inferences used for Mendelian traits (Árnason and Andersen, 2013). According to Árnason and Andersen (2013), the deCODE project—whose motivations are further examined in a later section—was entertained by the Icelandic government because participation promised medical advancements benefitting the entire population. By collecting the DNA of Icelandic volunteers, Steffánson curated a database of genetic variants which ultimately did not yield significant results on common disease and thus did not accumulate the expected financial profit, despite being responsible for considerable scientific literature (Árnason and Andersen, 2013). The corporation consequently declared bankruptcy in 2012 and was acquired by the biopharmaceutical behemoth Amgen (Árnason and Andersen, 2013).

Of course, the deCODE database has still amassed critical genetic information despite commercial failure; since the early 2000s, Steffánson's efforts have given rise to a wealth of medical publications (Gudbjartsson *et al.*, 2019; Gudmundsson *et al.*, 2019). One such recent study, by Gudbjartsson *et al.* (2019), examined genetic risk for diabetes and cardiovascular disease using deCODE data, and found that inherited lipoprotein A affects the risk for heart disease and increases risk for type-2 diabetes. DeCODE's Icelandic data has also been particularly valuable to behavioral genetics in studies of attention-deficit hyperactivity disorder (ADHD) (Gudmundsson *et al.*, 2019). When examined with similar Norwegian samples of ADHD patients, the data suggested that elevated occurrences of rare copy number variations were associated with increased risk for ADHD, which is considered among the same family of neurodevelopmental disorders as schizophrenia and autism spectrum disorder (Gudmundsson *et al.*, 2019). Such comparative studies are preferred by geneticists, as both populations are considered to be relatively homogenous (Árnason and Andersen, 2013).

ANCESTRAL IMPLICATIONS AND THE PURSUIT OF THE "IDEAL POPULATION"

In determining the suitability of an isolated population for genetic studies, assumptions of homogeneity can have critical implications for successful and legitimate research. Genetic links to common diseases are indicated in genomic data by differences at specific loci, and are easier to locate in populations with less overall variation (Annas, 2000). Important ethical precautions must also be taken when inferring homogeneity, as the mining of DNA from an entire nation may result in negative stigma if a shared association with a specific gene is implied (Annas, 2000). Moreover, Árnason and Andersen (2013) argue that population homogeneity is difficult to determine even with the increasing scope of genomic data available. In Iceland, where deCODE is responsible for the sole genetic database, the authority to determine the population to be adequately homogenous is essentially monopolized (Árnason and Andersen, 2013). Árnason further raises the concern that deCODE is capitalizing on the nationalistic culture of Iceland as a small country with shared heritage and sentiments of exclusivity in order to increase participation in the study (Lloyd, 2001). Similarly, Lloyd (2001) argued that deCODE encourages a genomic nationalism based on the possibility of shared markers for common disease and perhaps manufactures a homogenous identity.

The issue in determining Icelandic homogeneity is not a matter of differences in data but in the statistical methods used to interpret these results; among the following studies, the occurrence of linkage disequilibrium—where the association frequency of different alleles indicate non-random association—is unanimously acknowledged (Árnason *et al.*, 2000; Gulcher *et al.*, 2000). As a strong critic of deCODE, Árnason *et al.* (2000) argued that linkage disequilibria is indicative of population admixture and is responsible for the relatively high level of variation of mtDNA in comparison to other Europeans. Their study concluded that admixture creates the possibility for false positives in studies of pathological genetics, and that the assumption of Iceland as an ideal homogenous population should be scrutinized (Árnason *et al.*, 2000).

Gulcher *et al.* (2000), proponents of Steffánson

and deCODE, disagreed with Árnason's analysis of mtDNA, suggesting that any heterogeneity indicates that the early female Icelanders differ from their contemporary counterparts only by a large number of mitochondrial bases, with no implications for the genetic mixture of founding populations. Gulcher *et al.* (2000) explained that their previous efforts determined the founding population of females in Iceland to be relatively small, and only slightly larger than similarly isolated populations of Saami, Finns, and Basques, demonstrating that Iceland's current population is descended from few ancestors and can be considered homogenous for the purposes of genetic research. These findings were replicated by Helgason *et al.* (2003) through simulations of diversity at mtDNA hypervariable segment (HVS1) sequences, revealing a high frequency of HVS1 haplotypes and the absence of rare haplotypes in contrast with genetic data from most European populations. The study concludes that while admixture was present in founding populations, the unusual frequency distribution can be better attributed to genetic drift which produced greater homogeneity in modern populations (Helgason *et al.*, 2003).

In fact, genetic drift seems to be responsible for reduced mtDNA genetic diversity across Icelandic populations (Jones *et al.*, 2012). An examination of modern house mice in Iceland, Greenland, and Newfoundland, as well as ancient DNA from archaeological remains, show that the Icelandic mouse variety's low heterogeneity mirrors the movements and founder effect of early human populations in the North Atlantic (Jones *et al.*, 2012). Price *et al.* (2009) argued that low variation caused by the founder effect is also observable between regions of Iceland and attributable to recent genetic drift, not an ancient admixture of Norse and Gaelic influence. While Price *et al.* (2009) found Iceland to be relatively homogenous, there were also indications of slight diversity between subpopulations without a statistically significant distribution. Their results may also illustrate that the random distribution of Icelandic population data is less vulnerable to confounding, especially in comparison to other emigrated groups of European ancestry without a null distribution (Price *et al.*, 2009).

While the statistical methods for determining

population homogeneity remain disputed, Iceland has since been accepted as a reliable source for genetic databases and pathology research (Árnason and Andersen, 2013). The guidelines for genomic studies stem from a positional approach that assumes common diseases extend beyond nuclear units and are not present in all generations, unlike Mendelian diseases (Gulcher and Stefánsson, 2006). It is therefore harder to link common diseases to a specific genotype and a larger database becomes desirable (Gulcher and Stefánsson, 2006). According to Stefánsson (2003), over 160,000 Icelanders, approximately half the adult population, agreed to participate in the deCODE project and 99% of them consented to participate again in the study of other diseases. He also attributes the potential of deCODE to its genealogy database which includes records of 70% of all Icelanders since its settlement in 874 CE (Stefánsson, 2003). It is necessary, however, to consider not just the possibility for genetic research but also the efficacy and ethics of its potential results. In order to yield the most participation, DNA samples are nonlinkable and identified only by nationality, which leaves the potential for Iceland to be reductively associated with a specific negative phenotype (Annas, 2000). Another concern is the possible abuse of genetic data for eugenics agendas (Annas, 2000). Annas (2000) further considered the ethics of deCODE's business model as an American for-profit company, as it commodifies an individual's genome with no guarantee of financial benefit and medical advancements for the test community.

CONCERNS OF LEGALITY AND ICELANDIC GOVERNMENT RESPONSE

The risks of curating the DNA of a nation were largely unknown at the time of deCODE's establishment as it was the first database of its kind, and they prompted debate by the Icelandic government and citizens alike (Merz *et al.*, 2004). After deCODE was first presented to the government as a health sector database in 1997, it was not available in public records for a year until its introduction as a bill on the floor of Iceland's parliament, the Althing (Árnason and Wells, 2003). With an ambitious agenda for expedited approval, the bill aimed to secure exclusive rights to

genomic data with limited consent; the controversial strategy was met with strong criticism, especially from Árnason, who lobbied for *a priori* informed consent (Árnason and Wells, 2003). In order to pass the bill, a compromise was made that added a clause which assumed citizens' nonconsent on an opt-out basis, with unregistered or non-respondent citizens presumed to be willing participants (Árnason and Wells, 2003). Many participants consented to the release of genetic information with the understanding that deCODE and Icelandic authorities would ensure the confidentiality of all personal identifiers through one-way encryption when the data was referenced in longitudinal research (Árnason and Wells, 2003). Árnason and Wells (2003) argue that deCODE did not approach the release of data with informed consent in mind, as its leaders believed depersonalized records were sufficient in ensuring patient privacy and did not require the notification of individuals upon the release of their data to a scientific or academic venture within deCODE's exclusive licensing (Árnason and Wells, 2003).

Since then, deCODE has remained subject to legal scrutiny, with one retrospective analysis proposing clauses for the company's operating license to guarantee "(a) the safety of the data during their collection and subsequent processing; (b) that the data would be disconnected from individual identifiers prior to being incorporated into the database; and (c) that the processing of data in the database would not open the possibility of its reconnection with identifiable individuals" (Helgason and Gibbons, 2008, p.153). These stipulations were to be regulated by the Director-General of Public Health, a Monitoring Committee, an Interdisciplinary Ethics Committee, the Data Protection Commission (DPC), and the Data Protection Commission's Encryption Agency (Helgason and Gibbons, 2008). Despite heavy oversight, limitations to the democratic process have prompted outcry by Icelanders entrusting their health data to a parliament of only 63 representatives and a three-person DPC, with only one employee from an outsourced consultancy firm responsible for determining the genetic database's security (Helgason and Gibbons, 2008).

This bureaucratic failure and lapse in institutional accountability may be due in part to the

forementioned laxity in the original bill which included only vague requirements for organizational and technological standards for health databases (Helgason and Gibbons, 2008). Although the legislation stipulated that data must be encrypted to ensure personal privacy, it appears to have had an ambiguous understanding of which data is worth securing (Helgason and Gibbons, 2008). Moreover, Helgason and Gibbons (2008) argued that there is room for skepticism regarding the possibility of inferring personal information, both through shared phenotypes and the accessible genealogy of a fairly small country. Such concerns culminated in the Icelandic Supreme Court case *Guðmundsdóttir v. The State of Iceland* in which the appellant requested that the health records of her deceased father not be included in the database, citing the possibility that shared heritability could be used to make inferences on her own genetic information (Helgason and Gibbons, 2008). The court ruled in favor of the appellant, and their representatives maintained that given the sensitive nature of genetic databases and the inability of the law to prevent inference, it is impossible to ensure the confidentiality of participants (Helgason and Gibbons, 2008). The early trials of deCODE and their discourse with the Icelandic government can and should, however, signal to other such ventures the importance of establishing a transparent relationship with the public, and navigating potential controversies and ambiguous concepts early in the legislative process.

NEW APPROACHES TO POPULATION GENETICS DATABASES INTERNATIONALLY

In the last two decades, great strides have been taken to promote the ethical interests of all stakeholders in a number of emerging genetic databases (Elger, 2010). In Europe especially, careful consideration of legislative and operational frameworks is done to regulate ethical expectations and make international research more efficient (Merz *et al.*, 2004). As former Head of Genetics at Leiden University Medical Center, Gert Jan van Ommen, aptly stated:

The idea of setting biobanking guidelines is analogous to the standardization of Europe's rail system... Every country pays for its own train line, but

they have agreed to put their rails at the same distance so it's easy to go from the Netherlands to Greece without changing trains (Cited in Elger, 2010, p.252).

There is, however, no consensus or framework for balancing ethical concerns with research efficacy, especially with limitations on obtaining genetic data in order to protect participants (Elger, 2010). It is possible that moving forward, the definition of relevant data could be extended or that consent could be more loosely interpreted (Elger, 2010). Such flexibility is especially feasible as databases are now better established and attract public funding, and previous anxieties about consent are often less pressing as participants are more willing to release data without a detailed explanation of its use (Elger, 2010). I predict that ethical questions will enter new terrain, as genetic databases may extend their focus to new factors such as epigenetics.

Moreover, deCODE might do well to make note of earlier genetic databases. In fact, Québec had set an ethical precedent years earlier (Lloyd, 2001). While deCODE certainly encouraged other researchers to use databases with the assumption that the genes for a certain common disease would be universal among other populations, its research focused on ailments associated with developed countries and high life expectancies (Árnason and Andersen, 2013). As such, it appeared that deCODE's approach was not best aligned with research on populations with a high prevalence of Mendelian disorders (Lloyd, 2001). With the interests of a similarly affluent and supposedly homogenous population in mind, the Institut Interuniversitaire de Recherches sur les Populations (IREP) began a longitudinal genetic study on a subpopulation of Québécois based on genealogical materials gathered by historians in the past century (Lloyd, 2001). This group, the *pure laine* Québécois, settled into isolated villages during early French colonization of Canada and are especially interesting to researchers due to their subsequent low level of heterogeneity (Lloyd, 2001). The genealogical portion of the project, ongoing since 1972, compiled family trees in order to trace "disease genes" from the founder population (Lloyd, 2001, p. 45). Data were initially acquired without consent, as records of both the living and deceased belonged to

Québec up until 1993 (Lloyd, 2001).

Although a change in civil code made these records private following 1993, IREP researchers were still able to acquire vital statistics without consent so long as the statistics were not linked to medical records (Lloyd, 2001). It appears that these ethical and legal transgressions are integral to early genetic databases, and not unique to deCODE. Now, legal teams are especially attuned to participant consent, as well as ethics committees, benefit-sharing, and data protection (Austin *et al.*, 2003). This new approach is specific to European countries with socialized healthcare, reflecting their unique concerns that individuals may be found by a national database to have an unpreferred genotype and denied medical care (Austin *et al.*, 2003). Another fact of public genetic health systems is an attention to equitable shared benefits of participants as well as stakeholders seeking commercial profit, though there does not appear to be a generally accepted guideline for how fairness should be achieved and ethics committees tend not to have much leverage (Austin *et al.*, 2003).

Even today, databases are still wary of promising data privacy, as detaching personal identifiers from phenotypes would make gene-mapping virtually impossible (Austin *et al.*, 2003). An analysis of the Marshfield Clinic in Wisconsin by Austin *et al.* (2003) suggests an alternative method of ensuring data security; after receiving a certificate of confidentiality from the National Institute of Health and preventing the disclosure of any identifying genetic information through inquiry or subpoena, the Clinic codes and stores the project's data in an independent computer at another facility where it is not accessible online (Austin *et al.*, 2003). Such methods would likely be more complicated in longitudinal studies where data of an individual participant is compiled and analyzed over time. Furthermore, without any identifying measures, participants are also unable to completely remove their genetic information from a database should they wish to withdraw from a study (Price *et al.*, 2009).

Similarly, the efficacy of European regulations has been comprehensively studied, especially with regards to databases like UmanGenomics in Sweden, Geenivaramu in Estonia, and UK Biobank in the UK

(Gibbons *et al.*, 2005). A study by Gibbons *et al.* (2005) found that, while legal provisions outlined by the Declaration of Helsinki mandate that consent must be specific and with explicit motivations, it is not always feasible at the time of collection for the database to predict which researchers may later be granted access. Here, nuances of ownership versus intellectual property have arisen; “ownership” grants authority to determine how data may be accessed and profited on (Gibbons *et al.*, 2005). One might argue, however, that human genetics research should be a public venture without financial or personal gain in mind. The consensus in Europe is that genetic data can be reserved as an exclusive intellectual property right, with the copyright only applying to the design of a given database and its business model, but not to its contents (Gibbons *et al.*, 2005).

Conversely, some participants may choose to relinquish control over their data and remain uninformed about potentially sensitive genetic markers. Still, there remain instances where researchers obtained consent for a specific disease study and employed the data in another without notifying participants, as was the case in a genetic study of Havasupai Native Americans (Knoppers *et al.*, 2012). One can therefore assume that as the relationship between researchers and participants continues to develop away from the original government-partnered model of deCODE, and new opportunities in commercial direct-to-consumer testing grow in popularity, ideas about consent and property rights will be continually challenged.

DATABASES FOR PRIVATE USE AND THE COMMERCIALIZATION OF DNA

The structure of the most recent population genetics databases emerging in the United States are a far cry from that of deCODE. American genetic health services are necessarily unique from those in other countries with national healthcare systems. In order to collect data from a large population, researchers have collaborated with private healthcare providers, as the Marshfield Clinic did on a reduced scale (Kaiser, 2002). The Clinic initially received state funding as a non-profit for their database, and intended to funnel any profits

from patented findings back into research (Kaiser, 2002). As such, scientific advancement is likely the primary motivation for participants, who are not notified of any results (Kaiser, 2002). Private healthcare providers have worked with companies offering private DNA testing since the availability of RFLP and PCR technologies in the 1980s and 90s (Kirkpatrick *et al.*, 2016). Today, major genealogy companies utilize admixture analysis of SNPs in order to provide inferences on an individual’s ethnic background (Kirkpatrick *et al.*, 2016). This approach to consumer confidentiality is markedly different from research databases, as the full panel of SNPs is available to the consumer for download via an insecure internet browser for purposes of third-party assessment (Kirkpatrick *et al.*, 2016). Sensitive health data is not a major priority of these business models though, as their primary market is recreational genealogy (Kirkpatrick *et al.*, 2016).

Ethnic results of these at-home tests vary by producer (of which the most popular are AncestryDNA, 23andMe, and Family Tree DNA) as each uses their own contemporary population data and algorithms (Kirkpatrick *et al.*, 2016). The exclusive use of contemporary DNA presents its own challenges, as millennia of evolutionary mechanisms can be concealed by recent admixture and it is difficult to accurately distinguish any populations below the continental level (Kirkpatrick *et al.*, 2016). I do not find these limitations to be necessarily reflected in the companies’ advertising platforms, which suggest that consumers can use results to determine national, ethnic, or tribal relationships with a fair degree of certainty. Despite the unreliability of private DNA tests, there is little government intervention save for federal standards via certification by the Clinical Lab Improvement Amendments and the Food and Drug Administration which merely regulate quality control of lab kits, without controlling for reliable data (Kirkpatrick *et al.*, 2016).

This is not to suggest that commercial DNA tests are without ethical scrutiny; in fact, the wide accessibility of at-home testing has led to increased attention on familial consent (Wallace *et al.*, 2015). New applications of informed consent could arguably be extended beyond the individual consumer to their

relatives who could also be impacted by sensitive genetic information. AncestryDNA acknowledges this concern, with a notice that while collecting a saliva sample is not physically harmful, it is possible that relatives could be made aware of personal biological data (Wallace *et al.*, 2015). Interestingly, the genealogy feature of AncestryDNA suggests that consumers secure consent from relatives, but for DNA samples the onus is on the consumer as an individual (Wallace *et al.*, 2015). Even in the private sector, the collection of genetic material has a history of ethical disputes and evokes anxiety around being held responsible for consequences that Wallace *et al.* (2015) argue remain largely unknown over 20 years later.

ETHICAL QUESTIONS, POLICYMAKING, AND THE FUTURE

Tensions between public and private sectors surrounded deCODE's bid for exclusive commercial rights and the Icelandic government's release of medical data in the interest of public health (Merz *et al.*, 2004). Critics cited legal provisions of the Icelandic Constitution and European Economic Area regulations against the creation of monopolies with concerns that commercial and academic competition would be limited for the benefit of a private American investor (Merz *et al.*, 2004). Although deCODE agreed to fund Iceland's health sector database in exchange for sponsorship, it is possible that the government could have supported the database independently by employing strategies like those used for funding federal programs such as the US Affordable Care Act (Merz *et al.*, 2004).

Moreover, there are ethical concerns that deCODE's mining of Icelandic DNA for economic gain commodifies both human bodies and genetic material, and that their autonomy is threatened by government intervention (Pálsson and Rabinow, 1999). Geneticist Richard Lewontin worried that Icelanders were being manipulated by deCODE and the dominant force of American science, expressing disappointment that "a northern European" country could be bought by US capitalism (Pálsson and Rabinow, 1999, p. 17). Lewontin had also authored an article in the *New York Times*, titled "Iceland, the Nation of Clones" (Pálsson

and Rabinow, 1999, p. 17). *Anthropology Today* described this assertion as "orientalist," as American researchers appear to commodify remote and "unusual" populations, and maintained that this new era of global biotechnology requires careful social considerations (Pálsson and Rabinow, 1999, p. 17). They write that "molecularly inclined anthropologists" of the future will need to be cognizant of biocultural inequalities where the line between nature and society becomes blurred (Pálsson and Rabinow, 1999, p. 18). Moving forward, it is possible that the tendency of biological anthropologists to collect and categorize will become more interconnected within the realm of bioinformation, and the potential field of genetic ethnography will come with a wave of ethical literature for the next generation of anthropological researchers and government policymakers to consider.

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Women's Mating Strategies: Classical Views and Alternative Hypotheses

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INTRODUCTION

How do women choose the men with whom they mate and reproduce? Scholars from diverse fields have attempted to answer this question, creating explanations rooted in biology, cultural and evolutionary anthropology, economics and history (Belot and Francesconi, 2012; Gouda-Vossos *et al.*, 2019; Waynforth and Dunbar, 1995). Within evolutionary biology, one line of inquiry focuses on the reproductive strategies of non-human primate females to understand potential homologies in humans (Hrdy, 2000). Non-human primate females are subject to varied selection pressures within their ecological contexts as well as group dynamics that differ among species (Hrdy, 2000). Mating systems also differ among primate taxa, ranging from pair-bonding to "harem" polygyny to multi-male multi-female groups to polyandrous cooperative breeding in which females copulate with multiple partners (Hrdy, 2000). These mating systems have been studied within Darwinian natural and sexual selection frameworks to understand how intra and inter-species competition drives observed behaviors (Trivers, 1972). A generalization about female reproductive strategies across mating systems is that females are more discriminatory than males when choosing mates; this difference is based on gamete size/availability, along with gestation and lactation, which both place an energetic burden on females and make them unavailable as mates, contributing to a male-biased operational sex ratio (Trivers, 1972).

Based on theories of how non-human primates choose mates, classical views suggest that women seek men who can support them and their offspring with resources and protection, along with parental investment in the child (Benshoof and Thornhill, 1979). Thus, an adaptive strategy for women rests on finding the best possible mate and mating with him monogamously to ensure his paternity certainty so that he will not desert (Benshoof and Thornhill, 1979). Several

characterizations of women's reproductive strategies follow from this view: 1) that concealed ovulation is an adaptive trait because men must monitor the women to be as certain as possible of paternity, with proximity leading to increased resource provisioning, 2) that traits women find attractive are universal, and 3) that an adaptive and optimal strategy for all women will be to mate with one partner (Benshoof and Thornhill, 1979).

More recently, however, researchers have challenged these generalizations (Hrdy, 2000; Scelza and Prall, 2018; Walker *et al.*, 2010). Critiques have highlighted how observations of human behaviors do not conform to these generalizations and that studies investigating them lead to contradictory results (Scelza *et al.*, 2020). This essay will both review the arguments supporting classical views of women's reproductive strategies and discuss alternative views, highlighting not only the lack of universals in these reproductive strategies, but also that women may not be monogamous in all societies.

TRADITIONAL VIEW OF FEMALE STRATEGIES

Sexual selection operates inter-sexually to increase an organism's ability to attract mates to reproduce with, and is therefore distinct from natural selection, which describes a process in which species adapt to their environments for survival (Hosken and House, 2011). Natural selection favors traits that help organisms respond to stressors in their environments, such as being able to process different types of food in case of a shortage of preferred foods (Polak and Tomkins, 2021). Sexual selection, in contrast, operates on traits that members of the opposite sex use to evaluate potential mating partners, such that sexual selection results in traits for attraction as opposed to survival (Hosken and House, 2011). Darwin differentiated between these two processes, suggesting that some traits' function is to gain attention and

acceptance of copulation by the opposite sex, thereby linking selected traits directly to reproductive fitness, as opposed to environmental selection pressures which are indirectly linked with fitness (Jones and Ratterman, 2009). Using this framework, researchers have sought to identify human traits that function to attract opposite-sex mates, and to explain women's mating choices based on men's morphological traits and behavioral variations (Buss, 1989). Additionally, research has assessed whether reproductive strategies used by women may have evolved for functions unrelated to attracting mates (Pawlowski, 1999).

Using the Darwinian sexual selection framework, Bateman (1948) developed a hypothesis regarding human mating strategies in his study of fruit fly mating. Bateman (1948) found that males experienced higher reproductive variability than females did and thus predicted that females would be more discriminating in their mate choice because the majority of females reproduce, whereas males need to compete intra-sexually more than females to increase their fitness. Bateman adapted the findings from his fruit fly study to human beings, resulting in the now classically held view that women are the 'choosy' sex whereas men benefit from copulating with and impregnating as many women as possible (Benshoof and Thornhill, 1979). Women, specifically, are thought to choose men based on markers of genetic quality (Little *et al.*, 2007). Bateman's conclusion gave rise to studies that sought to identify phenotypes that constitute markers of 'good genes,' such as facial masculinity, intelligence and resource acquisition potential, among others (Havlicek *et al.*, 2020).

Using Bateman's 1948 study, Trivers (1972) considered the different morphological and behavioral investments that men and women undertake to reproduce, developing parental investment theory. Because women have a limited number of ova and must expend considerable time and energy during pregnancy and lactation, their reproduction is costly (Trivers, 1972). In contrast, men continue to produce sperm their entire lives and can be reproductively successful following a single act of copulation, underscoring how parental investment in creating and rearing children differs between the sexes (Trivers, 1972). Much research over the past three decades seeks to understand which traits

women value in men, with an interest in understanding how these traits may or may not differ cross-culturally, to understand how sexual selection has acted upon men and influenced women's strategies (Buss, 1989; Driebe *et al.*, 2021; Prokosch *et al.*, 2009).

Following this, Buss (1989) predicted that men's mate value would be based on cues of resource acquisition potential, including 'industriousness,' 'ambition,' and 'earning capacity.' To investigate this prediction, Buss (1989) surveyed women in 37 cultures to see whether these traits were in fact the most valued by women. This survey included 5,446 women in 33 countries with a mean age of 23 years (not all women were married and statistics for how many were married are not given), with sample populations varying in socioeconomic, educational, and urban versus rural location (Buss, 1989). Respondents were asked to rate specific characteristics ('good financial prospects' and 'ambition and industriousness') from zero to three—irrelevant in a potential male mate to indispensable in a potential male mate (Buss, 1989). It is not clear whether respondents were asked whether the potential mate was someone respondents would marry or date. Buss (1989) presented results through mean and standard deviation values for each trait from each sample population, but no average across all sample populations combined. The average importance of 'good financial prospects' ranged from a low of 0.94 in the Netherlands to 2.55 in Indonesia, whereas women weighed 'ambition and industriousness' between 1.41 (Netherlands) and 2.81 (Iran and Taiwan). Based upon these results, Buss (1989) concluded that the predictions for women's mate choice based on the Bateman-Trivers paradigm were upheld because the mean values exceeded 0, highlighting how women value men who can provide resources for them and their offspring.

Buss's (1989) paper seemingly evinced the universality of women's mating strategies and the importance of men's provisioning capability particularly. Since this publication, researchers have followed a paradigm that seeks to understand how women might maximize their reproductive success within a monogamous framework (Driebe *et al.*, 2021; Prokosch *et al.*, 2009). Generalizations of women's reproductive strategies resulting from the Bateman-Trivers-Buss paradigm are that 1) concealed ovulation is an adaptive

trait that functions to confuse men about paternity and enable women to pursue a dual-mating strategy (Jones *et al.*, 2019); 2) that women will choose men based on a set of universal traits deemed attractive, such as intelligence, resource holding potential, Major Histocompatibility Complex (MHC) compatibility and masculine appearance (Buss, 1989; Havlicek *et al.*, 2015); and, 3) that monogamy is an adaptive strategy for women within all sociobiological contexts (Benshoof and Thornhill, 1979).

CONCEALED OVULATION AS ADAPTATION

The traditional argument for why women conceal ovulation rests on the idea of using extended sexuality to confuse men about paternity in order to increase male provisioning of a woman and her offspring by increasing monitoring behavior (Benshoof and Thornhill, 1979; Strassman, 1981). The idea that women conceal ovulation and that this trait is linked to female mating strategies arose because female chimpanzees and bonobos, human's two closest living relatives, exhibit marked sexual swellings that signal their fertility status (Hrdy, 2000). Because of the stark differences between females of these species and women, researchers have sought to understand why women do not advertise ovulation (Havlicek *et al.*, 2015). The classic explanation suggests that concealed ovulation was sexually selected for in women because concealed ovulation promotes extended sexuality, making women able to be sexually active throughout the menstrual cycle (Grebe *et al.*, 2013). By having intercourse during periods of infertility, women can confuse the men they mate with about the paternity of their offspring, causing men to spend more time mate guarding and provisioning the woman to mate with her more frequently and increase their chances of fertilizing her ova (Jones *et al.*, 2019). The traditional view contrasts the adaptive benefits of concealed ovulation with men's theoretical behavior if women did not conceal ovulation; Benshoof and Thornhill (1979) suggest that explicit ovulation would enable a man to impregnate a woman and then desert her to copulate with other ovulating women. Although the woman is pregnant, this behavior nonetheless decreases the women's lifetime fitness because the man would not provision her as much, making her rely on her own foraging throughout pregnancy and lactation—during

which she and her infant are vulnerable to ecological and behavioral stressors from other animals (Benshoof and Thornhill, 1979).

A second proposed benefit of concealed ovulation in women is that it enables women to adopt a dual-mating strategy in which they engage in extra-pair copulation while being pair-bonded to their provisioning man (Jones *et al.*, 2019). This strategy relies on women being able to successfully confuse men about their paternity status, such that the pair-bonded man is unable to discern if the woman's offspring are his, and he provisions them regardless (Havlicek *et al.*, 2015). Specifically, a woman can mate with men who have higher genetic quality than her partner, potentially increasing her fitness if she can both secure provisioning from her partner and pass on better genes from her secondary partner (Havlicek *et al.*, 2015); Jones *et al.*, 2019). The dual-mating strategy rests on women being able to ascertain whether her long-term partner will reliably provision her and her offspring, sacrificing higher fitness (by mating with one as opposed to multiple women) in exchange for paternity certainty (Havlicek *et al.*, 2015); Jones *et al.*, 2019). This strategy rests on women mating with other men and conceiving their offspring, thus decreasing the provisioning man's fitness, leading one to question why sexual selection has developed mechanisms for men to detect whether their partner's offspring are their own. Nonetheless, Strassman (1981) argued that concealed ovulation evolved to increase paternal care of offspring. An implication of dual-mating is that women may shift their preferences towards more masculine men (considered to exhibit cues of high genetic quality) during the fertile phase of the menstrual cycle, and then return to preferring men with higher resource acquisition potential during non-fertile phases (Havlicek *et al.*, 2015). Such a strategy rests on concealed ovulation being a sexually selected trait that increases women's fitness at the expense of the fitness of a woman's provisioning partner (Havlicek *et al.*, 2015).

There are, however, alternative explanations for how concealed ovulation benefits women. One such benefit is that confusing men of paternity decreases infanticide risk; Hrdy (2000) argued that ancestral male *Homo sapiens* killed infants who could not be their offspring to quickly return the woman to her fertile state

and then mate with her (a practice that occurs in many non-human primate taxa). Concealed ovulation can decrease the likelihood of infanticide via extended sexuality, as men would be less able to ascertain whether a woman's infant was his child if he had mated with her previously (Hrdy, 2000). Similarly, concealed ovulation could benefit the woman through the provisioning mechanism highlighted above, or by allowing her to mate with a potentially aggressive man outside of her fertile period, decreasing the likelihood of conceiving his child and allowing her a higher degree of mate choice if she can successfully attract a preferred mate and mate with him in her fertile period (Jones *et al.*, 2019). Hrdy (2000) views concealed ovulation as an ancestral human state, and sexual swellings in chimpanzees and bonobos as derived traits, in contrast to the traditional view which postulates that ancestral women exhibited ovulation. Since infanticide occurs across primate taxa, (relatively) concealed ovulation may be a general feature, with some species developing sexual swellings for alternative reasons (Hrdy, 2000).

The notion that concealed ovulation represents an adaptation is prominent in the literature because of the desire for an explanation of the markedly different signaling of ovulation in humans versus chimpanzees and bonobos, as well as the observation that women shift their preferences for men across their cycles (Little *et al.*, 2007). It has been questioned, however, whether concealed ovulation is an adaptation for fitness at all, suggesting that it may be an evolutionary by-product. Pawlowski (1999) argued that concealed ovulation may have developed in hominins in association with physiological changes that occurred during the transition to bipedalism. Pawlowski (1999) suggested that sexual swellings in humans were mild and that upright locomotion shifted the location of female genitals to be less visible, causing sexual swellings to become unnecessary and inhibitive of bipedalism, and therefore selected against trait. Further sociobiological changes in human evolution that may have rendered conspicuous ovulation redundant include the increased population density of hominin groups living in the open savannah, as well as the need to conserve water for thermoregulation (Pawlowski, 1999). Specifically, Pawlowski (1999) argues that sexual swellings in the genital area would interfere with sweat evaporation

because these swellings would not be exposed to the sun. Pawlowski's (1999) explanation underscores how currently expressed traits may result from selection pressures in ancestral environments that are unknown to current researchers.

Another argument that concealed ovulation may be a by-product considers whether concealed ovulation is merely a physiological byproduct of shifting ovarian hormones throughout the menstrual cycle (Havlicek *et al.*, 2015). Havlicek *et al.* (2015) base their argument on the idea that women signal their fertility status through behavioral or physical changes during ovulation, hypothesizing that concealed ovulation may exist in women simply as a result of shifting levels of sex hormones throughout the menstrual cycle. The authors suggest that changes in women's attractiveness and propositioning behavior to masculine men across the menstrual cycle result from shifting levels of sex hormones (Havlicek *et al.*, 2015). This change may shift preferences to masculine men because masculine features may signal higher genetic quality, which is desirable for fertile women (Havlicek *et al.*, 2015). Therefore, any changes that do occur in women would happen regardless of sexual selection for concealed ovulation (Havlicek *et al.*, 2015). They further argue that focusing on within-woman shifts in mating strategies over time misses the bigger picture of how women engage in intra-sexual competition to attract mates (Havlicek *et al.*, 2015). Women exhibit their fertility status through cues such as youth, facial symmetry and averageness, and waist to hip ratio—each of which differs between women according to estrogen levels—and these between-woman markers may play a bigger role in mating success than within-woman changes in fertility (Havlicek *et al.*, 2015). The authors explain women's attraction to specific men with high quality genes (with strength and facial attractiveness as proxies) as being unrelated to resource provisioning, which they argue is more logical from a fitness perspective than explanations in which women privilege resources at the expense of good genes (Havlicek *et al.*, 2015).

The argument that concealed ovulation is a by-product of unrelated adaptations or physiological mechanisms is persuasive given the lack of evidence showing that women who conceal ovulation “better” have higher fitness than women who exhibit ovulation

(how women conceal or exhibit ovulation is undefined in the literature). Evidence for the fitness benefits of a trait is necessary for determining whether a trait is an adaptation, and arguments suggesting concealed ovulation is an adaptation do not reach this standard (Haufe, 2008). Moreover, the behavioral implications of concealed ovulation (such as widespread cuckoldry through paternity confusion) must be shown to exist in statistically significant numbers. Instead, men whose fitness is directly affected by such a practice would have evolved mechanisms for ascertaining women's fertility or their paternity of offspring, such that the actual benefits of concealed ovulation would be negated.

WOMEN CHOOSE MEN BASED ON A SET OF UNIVERSALLY VALUED TRAITS

The traditional view of women's mating strategies holds that women prioritize men who can best provision the woman, which in turn suggests that women will be attracted to men who signal their resource acquisition potential (Buss, 1989). To investigate whether there is evidence consistent with this view, scholars have studied traits deemed to correlate with resource holding potential (such as intelligence) and traits deemed to correlate with physical attractiveness (such as MHC compatibility), along with fluctuating preferences for masculine men across the cycle (Havlicek *et al.*, 2020; Prokosch *et al.*, 2009). Empirical studies aimed to ascertain whether these supposedly attractive traits are in fact valued by women have led to contradictory results, and may suggest that the attractiveness of these traits or the preference-shifting behaviors may be context-dependent as opposed to universal (Havlicek *et al.*, 2020; Prokosch *et al.*, 2009).

MHC compatibility refers to dissimilarity of the genes of the major-histocompatibility complex—an immune response function that has been hypothesized to be identifiable through olfactory cues and influential in human mating choices (Havlicek *et al.*, 2020). MHC genes are critical in adaptive immune responses to novel or hostile pathogens and are more polymorphic than other sections of the chromosome, signifying high genetic variation between individuals for MHC genes (Havlicek *et al.*, 2020). Because of the importance of immune response in organism survival, Wedekind *et al.* (1995) hypothesized that there should be a mechanism

for detecting MHC profile in other humans, and that this compatibility may influence mating decisions due to the evolutionary benefits of genetic diversity in immune function.

Wedekind *et al.* (1995) undertook a study to ascertain whether women could discern MHC profile through body odors and whether they were preferentially attracted to particular profiles. The study asked 44 male volunteers to wear a t-shirt to sleep for two nights and to refrain from behaviors that might induce particular smells such as bathing, using cologne, or engaging in sexual activity (Wedekind *et al.*, 1995). The 49 female volunteers were then asked to smell the six different t-shirts and rank the t-shirts according to the "sexiness" of their smell (Wedekind *et al.*, 1995). The researchers used serological testing to determine MHC profiles for each participant, and matched the women's rankings with the women's and men's MHC profiles to determine whether a relationship between MHC profile and "sexy" smell existed (Wedekind *et al.*, 1995). The results indicated that women preferred t-shirts of men who had MHC profiles more dissimilar to their own, suggesting that MHC compatibility may be significant in women's mating choices (Wedekind *et al.*, 1995).

The results of the study by Wedekind *et al.* (1995) show strong evidence consistent with the hypothesis that markers of immune function may influence mate choice, given the clear evolutionary benefits that diversity in immune response would induce. Despite this finding, a more recent meta-analysis by Havlicek *et al.* (2020) found no significant relationship between MHC compatibility and women's mate preferences. The studies assessed by this meta-analysis undertook MHC typing of real-life married couples (mainly from the U.S. and Western Europe) and surveyed them on relationship satisfaction, finding that while the couples were on average relatively MHC dissimilar, there was no relationship between this variable and self-reported satisfaction (Havlicek *et al.*, 2020). Havlicek *et al.* (2020) explained this finding by noting that given the high degree of polymorphism within MHC genes and a sufficiently large population without inbreeding, any mate should be relatively MHC dissimilar, making this variable insignificant in mating decisions. The authors suggested that studies of MHC-dependent mate preferences should focus on small-scale

indigenous societies in which the pool of potential mates is much smaller, in order to assess whether women can in fact discriminate between MHC compatible men and whether they more often choose more MHC dissimilar men as mates (Havlicek *et al.*, 2020).

In congruence with the argument that women are attracted to MHC dissimilar men, it has been suggested that women's preferences for more genetically superior (stronger and with greater facial symmetry) men increase during fertile periods of the menstrual cycle (Little *et al.*, 2007). Considering the dual-mating hypothesis described earlier, the notion that women may prefer more masculine men during the fertile stages of their cycles is reflects the notion that women may try to conceive with men of higher genetic quality while remaining pair-bonded to provisioning men who may have lower genetic quality. Little *et al.* (2007) predicted that women's preferences for more masculine ("sexier") men would increase during fertile periods, and would also positively correlate with women's interests in short term relationships (defined as casual sexual relationships). The 97 women volunteers who were in the late follicular phase of their menstrual cycle (identified through self-reported data on their date of last period) were presented with 10 paired images of a particular man (full face and body photographs) in edited 'masculinized' or 'feminized' forms (Little *et al.*, 2007). They were then asked to choose the preferable form for all 10 men (Little *et al.*, 2007). The results indicated that women preferred the masculinized version on average for both short and long term relationships, which the authors found to be consistent with their hypothesis that women are more attracted to masculine men during fertile periods (Little *et al.*, 2007).

Notably, this study by Little *et al.* (2007) did not survey women in the same way during non-fertile periods, which may mean that the results of the study overestimate the purported relationship between fertility and preferences. To test the hypothesis in question, the researchers should have investigated whether women have significantly different preferences for men's masculinity while in fertile and unfertile periods. Otherwise it is not possible to know whether the particular women in the study simply had higher preferences for masculine men than the general population. Further, Havlicek *et al.* (2015) argue that

between-woman variation in hormone levels is more important in mate selection than within-woman shifts in fertility, because a woman presents herself in only one state at a time. Therefore, Havlicek *et al.* (2015) suggest that studies showing women to appear more attractive during fertile periods may be observing physiological mechanisms rather than sexually selected traits. In real life women are never presented with a 'masculinized' or 'feminized' version of the same man; they only meet the actual man, potentially in different contexts (as described in the section on concealed ovulation). It may be true that women are more attracted to masculine men given the logical correlation between markers of physical attractiveness, health, and high genetic quality (Jones *et al.*, 2001); yet studies like that of Little *et al.* (2007) employ methods that are unlikely to lead to results showing evidence consistent with this hypothesis, as these studies ask women to undertake "mating decisions" that never actually happen.

Intelligence is a trait viewed as being an important factor in women's mating decisions, due to the potential correlation between intelligence and ability to acquire resources (Driebe *et al.*, 2021). Interestingly, two studies published in the same journal using relatively similar methods led to contradictory results regarding the importance of intelligence in men's attractiveness (Driebe *et al.*, 2021; Prokosch *et al.*, 2009). Prokosch *et al.* (2009) found that women value intelligence in potential mates, whereas Driebe *et al.* (2021) found that women can detect men's intelligence but do not factor this trait in when choosing between potential mates. The methods used in each study consisted of having male volunteers read newspaper headlines aloud while being recorded, and then showing these videos to women volunteers who decided if they would engage in a short (brief sexual relationship), long term relationship with the men (marriage), or neither (Driebe *et al.*, 2021; Prokosch *et al.*, 2009). The results from the study by Prokosch *et al.* (2009) indicated that women preferred men of above-average intelligence for long-term, monogamous relationships (marriage). The authors interpreted this as reflecting the fact that intelligence signals a higher resource earning potential, which conforms to the Bateman-Trivers-Buss paradigm (Prokosch, 2009). In contrast, Driebe *et al.* (2021) found contradictory results based on similar methods; the results indicated that

women did not consider men they perceived as more intelligent necessarily more attractive, suggesting that perceived intelligence did not increase men's mate appeal (Driebe *et al.*, 2021).

How should such contradictory results be interpreted? It is possible that the method these studies used leads to results that are difficult to replicate because women are asked to choose between potential mates in ways that never occur in real life. In real life women meet men through different contexts, such as in school, as neighbors or family acquaintances, or through matchmakers/other avenues. These contexts impact the impressions or conversations women have with men, and therefore lead to different perceptions of attractiveness for each man a woman meets, whereas developing a standardized rubric to discern attractive traits is difficult to ascertain experimentally. Additionally, many studies explicitly ask women to decide whether they would have a short or long-term relationship with a potential mate, with the goal of determining whether women shift their preferences depending on the type of relationship (Driebe *et al.*, 2021; Little *et al.*, 2007; Prokosch *et al.*, 2009). Although women may indeed engage in differently-styled relationships, it is unlikely that this question elicits the results researchers are looking for because relationships develop organically and a woman may not decide, especially before having met someone, whether she seeks a 'short' versus 'long' relationship with a particular man. Another issue is that participants are being asked what they think they would do, rather than observing their actual behavior, which may differ.

Studies such as described above do not take such contexts into account and therefore cannot model mating decisions accurately. In addition, one might question the validity of the variables that researchers use as proxies for traits such as intelligence. Reading newspaper headlines aloud may or may not correlate with intelligence, and no evidence that links this behavior with intelligence is presented in either study. Basing results on theoretically undefined mechanisms, and extrapolating to how all women make mating decisions will likely result in mistaken or exaggerated generalizations. Rather, studies that can better replicate the real-life contexts in which women meet and discriminate amongst potential mates can likely explain

mating decisions better than studies that employ methods that are divorced from such real-life contexts.

A study undertaken in Namibia of members of the Himba pastoralist tribe found that many traits identified by the Bateman-Trivers-Buss predictions were upheld in this population, showing that such predictions may accurately describe women's mating choices in some circumstances (Scelza and Prall, 2018). Scelza and Prall (2018) led a focus group of three to five women, asking them to freely list traits they would find attractive in formal and informal partners. The authors distinguished between the two types of partners because in Himba society extra-pair relationships are normal and accepted by both sexes; thus, Scelza and Prall (2018) hypothesized that desirable traits may differ between these two relationship styles. Scelza and Prall (2018) distinguished formal/informal from the commonly used short/long term, given that in Himba society most adults have long term informal partners outside of marriage, which differentiates these relationships from the 'fling' connotations of short term mating used in much of the literature on western societies such as those by Prokosch *et al.* (2009) and Driebe *et al.* (2021). After the focus groups developed their list of important traits, community members were asked to rank order the options for informal and formal partners (Scelza and Prall, 2018). Rank ordering was chosen rather than rating the traits individually, because ranking requires respondents to make discrete decisions, stressing the relative importance of particular traits (Scelza and Prall, 2018).

Himba women appear to seek husbands (formal) who are wealthy and boyfriends (informal) who are respectful, a distinction that conforms to the traditional predictions of women's mate choice with regards to husbands (Scelza and Prall, 2018). For husbands, wealth is followed by being respectful and hard-working, suggesting that women seek men who can help provision them and their children as well as treat the women well (Scelza and Prall, 2018). In boyfriends, women look for men who are respectful, generous, and wealthy (in order of importance), highlighting how women may seek provisioning from multiple partners (Scelza and Prall, 2018). The traits desirable in husbands and boyfriends do not differ much except with regards to the importance of respect, which may reflect a

woman's desire to enter into an informal relationship with a compatible man who treats her well, while wealth is more important for husbands (Scelza and Prall, 2018). These results imply that traits identified through the Bateman-Trivers-Buss paradigm may indeed be significant in women's mating decisions, although the Himba study highlights the importance of context in such decisions.

MONOGAMY MAY NOT BE A UNIVERSAL FEMALE STRATEGY

The Himba study by Scelza and Prall (2018) also challenges the aforementioned traditional view that women mate monogamously to ensure provisioning by their partner, given the acceptance of non-monogamy in Himba society. Both anthropological fieldwork and morphological traits suggest that polyandry may benefit women within specific sociobiological conditions, thereby disrupting the monogamous paradigm of universal female strategies (Ellsworth *et al.*, 2014). One physiological trait that signals potential polyandrous mating in a species is sperm competition, in which males' sperm compete to fertilize an egg inside a female's reproductive tract (Hrdy, 2000). Sperm competition is possible only if females mate with multiple males, and a key marker of sperm competition in a species is the size of testes relative to overall body size; males of species in which females mate multiply have larger testes than species in which females mate with only one male (Hrdy, 2000). In addition, a relatively high ejaculatory sperm count may accompany multiple mating and signal sperm competition (Hrdy, 2000).

According to Hrdy (2000), humans have relatively large testes for their body size, which suggests that polyandry was present during human evolutionary history. Hrdy (2000) questioned whether women may not benefit in the same way as other animals by mating polyandrously. She argued that such behavior may increase the likelihood of conceiving with a man of higher genetic quality, or increase male provisioning by forming consortships with multiple men—which would be particularly critical during the postpartum period when women and infants are highly vulnerable and require considerable care (Hrdy, 2000).

Evidence from small-scale societies suggests polyandry can even be codified within a culture's mating

practices and may benefit both male and female fitness (Walker *et al.*, 2010). In some indigenous societies, particularly in Amazonia and lowland South America, polyandrous mating is codified within societal norms via the concept of partible paternity (Walker *et al.*, 2010). Through partible paternity beliefs, children are considered to be the biological offspring of multiple men, all of whom had sexual relations with the mother (Walker *et al.*, 2010). According to belief, a fetus is created once the woman has enough sperm in her reproductive tract, with the sperm of multiple men mingling until the threshold is met and collectively fathering the child (Walker *et al.*, 2010). Fatherhood in many partible paternity societies is codified through *couvade* practices upon birth of the child: rituals a father engages that seek to mimic the mother's labor pains, such as remaining bedridden and isolated from the group and public rituals after isolation (Walker *et al.*, 2010). All of a woman's male partners participate in such rituals and are therefore considered co-fathers of the child (Walker *et al.*, 2010). This system deviates substantially from the traditionally held view of human mating strategies, wherein men should not tolerate extra-pair copulation, and women should mate monogamously with a man of high resource holding potential to ensure his provisioning (Benshoof and Thornhill, 1979).

Believing in partible paternity may facilitate multiple mating and increase women's fitness by providing multiple fathers as an insurance policy in case of father mortality and solidifying male alliances which may benefit group living (Walker *et al.*, 2010). Walker *et al.* (2010) undertook a meta-analysis of studies examining the partible paternity's fitness benefits for women, and found evidence consistent with the hypotheses that women benefit by acquiring multiple male investors, developing social bonds with multiple men, and increasing offspring genetic diversity (which insures against a partner's potentially bad genes). The evidence for the multiple investors hypothesis is based on quantitative studies that suggest offspring with multiple fathers have higher average survival rates due to greater provisioning than offspring without co-fathers, which is a clear fitness benefit to both males and females (Walker *et al.*, 2010; Ellsworth *et al.*, 2014). Evidence for the social benefits to women from partible paternity comes from the practice of women giving gifts to their male partners,

which is also evidence against the resources for sex hypothesis (Walker *et al.*, 2010). High status men are also found to have more female partners and therefore engage in co-fatherhood more frequently, which Walker *et al.* (2010) promoted as evidence for the genetic diversity benefits to women from partible paternity (assuming high status men have better genes), though this hypothesis was questioned by other studies though, as is discussed below.

To further study how partible paternity benefits women's fitness, Ellsworth *et al.* (2014) studied the Ache society of Paraguay. Their study sought to understand co-father relationships to ascertain how women chose the co-fathers for their offspring, which can either increase or decrease genetic diversity of offspring depending on how co-fathers are related (Ellsworth *et al.*, 2014). If co-fathers are found to be more related on average than any two men in Ache society, then alternative explanations for female polyandry are necessary (Ellsworth *et al.*, 2014). Ellsworth *et al.* (2014) predicted that women would mate polyandrously if multiple male investors provisioned all of a woman's offspring and that partible paternity increases offspring genetic diversity. They employed structured interviews of men and women to understand how resources are shared, and used genealogical records and reconstructions to assess male relatedness (Ellsworth *et al.*, 2014). The multiple investor hypothesis was supported, as co-fathers helped provision all of a woman's offspring and these offspring had lower mortality rates than children with only one father, corroborating results from Walker *et al.* (2010) (Ellsworth *et al.*, 2014). Contrary to the second hypothesis, co-fathers were more related on average than males who were not co-fathers, which would decrease the genetic diversity of offspring given that the children would have the genes of (for example) the brother of the woman's primary partner, as opposed to an unrelated co-father (Ellsworth *et al.*, 2014). Ellsworth *et al.* (2014) explain this discrepancy between their hypothesis and their findings by suggesting that co-father relatedness supports male alliances to jointly provision offspring of "shared" women, whereby men support their relatives' inclusive fitness.

CONCLUSION

This essay considers the strategies women use to attract and choose men, which is a key factor in their reproductive success and is therefore crucial to understanding human evolution. The traditional framework for analyzing women's strategies uses Darwinian sexual selection to identify traits that women should consider important in men. As demonstrated in this paper, alternative hypotheses postulate, however, that women's mating strategies may rest on mating polyandrously in a variety of relationship styles, rather than through pair-bonding. Indeed, evidence from Amazonia and Himba societies highlights how decisions for mating, reproduction, and relationships are more intricate than standard Western-based models can explain (Ellsworth *et al.* 2014; Scelza and Prall, 2018; Walker *et al.* 2010). Overall, this essay shows that contrary to traditional theory, women's mating strategies are far from universal, as clear examples of adaptations to sociobiological niches and variation in strategies exist. Further research should assess the interplay between culture and mating strategies to understand how women negotiate their fertility and fitness in the context of cultural constraints.

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