INTRODUCTION

In the study of human societies certain questions have exercised the minds of scholars for thousands of years. These include:

- Why are some societies so much wealthier than others?
- Why do some groups within a society suffer disadvantage?
- Why do wars occur?
- Why do economic recessions occur?
- Why do birth rates tend to decline in affluent societies?
- Why do some countries form stable democracies and others do not?
- Why do certain peoples rise to power and prominence?
- Why do civilizations fall?

Each of these questions has attracted multiple answers. For example, the rise of the West has been attributed to Protestant Christianity, the Enlightenment and the Industrial Revolution. The decline and fall of nations and empires has been explained as the result of economic stagnation, social pressures, disease and climate change. Populist historians have explained historical change as the result of great leaders such as Augustus, who brought an end to Roman civil war, Charlemagne, who established the Frankish Empire, Napoleon as conqueror of Europe, and Hitler as a crazed demagogue driving his people to destruction.

While these explanations are diverse they share one thing in common—they are not testable empirically. Even the most rigorous historical analysis can do little more than show that selected factors trend together and are possible causes of change. Historians may argue that the Second World War was launched by Hitler's personality or the Versailles Treaty or the economic crisis of the Weimar Republic, but short of repeating history *without* Hitler or the Versailles Treaty there is no way to be certain.

The theory presented in the following pages sees changes in social, political and economic behavior as reflecting changes in temperament. It accepts the prevailing view that temperament is a behavioral and emotional state that varies among individuals, is relatively stable over time and situation, is biologically based and appears early in life, but is influenced by parenting style and other environmental variables which condition how the inherited temperament is expressed.[1]

Where it differs from other approaches is in seeing the prevailing temperament of the population as the key to all those questions asked earlier. It is far more important than political and economic institutions, the decisions of leaders, or *any other factor*.

This theory also identifies the key aspects of temperament for this purpose as two separate but related biological systems which help animals adjust their attitudes and behaviors to changes in the environment.

One of the systems is triggered by relatively mild yet chronic food shortage, the other by occasional famine or predator threat. Both work via physiological signals that influence the expression of genes. In turn, behavioral change renders individuals more likely to survive and prosper. For example, mild food shortage leads animals to drive away members of their species and become more active and exploratory—behaviors that increase their chances of survival in environments with limited food.

But these systems can be triggered in other ways. Human cultures have developed codes of behavior, especially related to religion, that have the same effect as calorie restriction. These codes conflict with "natural" human inclinations but have been strengthened by competition between cultures. They change human temperament in a way that has made the rise of farming possible, along with wider political loyalties and more advanced economies—what we term 'civilization.'

These codes of behavior include fasting, religious rituals, patriarchy, and (above all) the restriction of sexual activity. By mimicking the physiological effects of hunger they help individuals and societies to survive and prosper.

[1] Jan Kristal, *The Temperament Perspective, Working with Children's Behavioral Styles* (Paul H. Brooks Publishing, 2005); Jerome Kagan, *Galen's Prophecy: Temperament in Human Nature* (Basic Books, 1994); Mary Rothbart, David Evans & Stephan Ahadi, "Temperament and Personality: Origins and Outcomes," *Journal of Personality and Social Psychology* 78 (1) (2000); This view is distinct from the ancient Greek concepts of four bodily "humours" (choleric, melancholic, phlegmatic and sanguine) widely accepted up to the eighteenth century; Robert Stelmack & Anastasios Stalikas, "Galen and the Humour Theory of Temperament," *Personality and Individual Differences* 12 (3) (1991).

To understand how this works, contrast the survival strategies of hunter-gatherers with those that drive success in civilization. Hunter-gatherers normally need only a few hours a day to find enough food, and the work is varied and interesting (especially for the men as hunters). They spend much of their time socializing, which develops bonds that aid group defense. Individuals who work harder but are less sociable would probably have fewer surviving children than others.

In a civilized society the state tends to handle defense, and socializing detracts from the crucial work of making a living. Thus, an individual who works harder and socializes less is likely to have *more* surviving children. Success in different social environments thus requires a different form of temperament.

Civilized societies also require physical technologies such as agriculture, metalworking, writing and trade. Yet, on their own, these technologies fail to explain why some civilizations rise and why others fail.

The changes in human behavior and temperament that are induced by cultural strategies and practices are rooted in epigenetics. This means that environmental influences, especially in early life, alter the level of activity and expression of key genes. These in turn affect behavior and temperament, including attitudes toward authority, capacity for work, economic and mechanical skills, and creativity.

The development of civilization thus depends on developing not only physical technologies but cultural technologies, especially religions. For example, if a religion induces behavioral change such that the society farms more productively, has more surviving children, and organizes itself into a large state, it is likely to expand and conquer its neighbors.

A weak point about these cultural systems is that they are vulnerable to the effects of abundance and population density. Wealthy urban societies with plentiful food tend to abandon ascetic behaviors, such as restrictions on sexual activity, which mimic the effects of food shortage. This in turn leads to society-wide change in temperament and behavior which undermine success. In effect, the greater the wealth and density of a society's population, the harder it is to maintain the cultural strategies responsible for the society's rise. In the chapters to come we propose that the collapse of civilizations, along with their replacement by people from less-developed societies, can be understood in this way.

This is a theory of mammalian social behavior which offers a novel and robust understanding of human history. Because it is a historical theory based on biology, it is given the name “biohistory.”

While initially developed from the study of human societies, the biological basis of the theory makes it possible to generate hypotheses that may be tested in both animal and human populations. To continue the example given earlier, there are a number of theories for the origin of the Second World War that are broadly consistent with the evidence, including the personality of Adolf Hitler and resentment against the Versailles Treaty. Biohistory proposes a different reason—that it was (in part) the result of anxiety transmitted to infants born at the close of the 1914–18 war, which caused a permanent epigenetic change that made them more aggressive. When these young men reached their early twenties they brought about a more militaristic tone to society which helped launch another war. So far this is a standard historical theory, broadly consistent with the evidence, but no more.

The key difference is that this particular theory can be tested quite rigorously by *testing the men born in 1917–18* for a specific epigenetic signature associated with aggression in rats *and* people, which should be more prominent in this cohort than in those born earlier or later. If too few subjects are available, the same could be done for Chinese born in 1948–49 or Europeans born in 1944–45. To the extent that this pattern is *not* found, the theory is weakened or must be modified; to the extent that it is, the theory is confirmed.

There are hundreds of other potential tests that could be done, some of which are detailed in the final chapter. Clearly, not every application of biohistory can be tested in this way since most of it relates to the distant past, but that is no different from any scientific theory. Physicists assume the laws of gravity apply to distant galaxies as they do on Earth, even though there is no way to test them directly. The measure of any scientific theory is not that every application must be tested but that it gives rise to testable hypotheses through which it *can* be tested, in the sense that it may be falsified or confirmed. In this sense, as a theory of history, biohistory is unique.

Chapter one reviews the family and social patterns that are present in civilized societies, including nuclear monogamous families, control of children and restriction of sexual activity. Studies of non-human primates in their natural environments, principally baboons and gibbons, show that many of these behaviors are associated with food-restricted environments. Animals adapt to such environments by delaying breeding, reducing group size, and moving from promiscuous mating towards nuclear monogamous families. It is a physiological response which allows populations to adapt quickly to food shortage, but to abandon such behavior when food is once more plentiful.

Chapter two presents laboratory studies on the effects of mild food restriction on rats. Among other affects it improves maternal care, reduces sexual activity and increases exploration. These studies show how food restriction during infancy changes the activity levels of genes which affect the behavior and the biochemistry of animals during later life. These changes may be inherited by an individual's offspring, at least partly through changes in parental behavior.

Chapter three examines how human cultural norms, especially control of sexual activity, have the same effect as calorie restriction. Religion drives the development of civilization through its influence on behavior and temperament, at least as much as technologies such as metalworking and trade. We refer to this "civilized" temperament as "C."

Chapter four uses zoological and ethnographic evidence to introduce a second set of characteristics that are distinct from those related to C. These include vigorous aggression, intolerance of crowding, hierarchical cooperative social organization, male domination of females, and a switch from indulgence and protection of infants to rejection of juveniles after weaning. This behavior is labeled "V" (for vigor) and is an adaption to environments where food is generally plentiful but with occasional famines. Such environments require mutual defense and fast population growth. V is triggered by occasional but severe stresses, such as famine or predator attack.

Chapter five further develops the concepts of C and V. It focuses on how cultural practices which promote C and V have very different effects depending on the age of exposure. Control of children during early childhood increases "Infant C," which renders individuals open to change and being skilled with machines. "Child V," which results mainly from experience of authority and punishment during late childhood, renders people more traditional and accepting of authority. Punishment of children also raises the level of stress in the society. Ethnographic case studies are reviewed to further test the concepts of C and V. The chapter shows that cultural norms and childrearing patterns influence adult temperament, which in turn determines political systems and levels of economic success.

Chapter six traces the rise of C in England over more than five centuries. Changes in age of puberty, family patterns, attitudes towards sex, work habits and increased control of children, especially infants, are documented. The striking success of the Industrial Revolution during the nineteenth century is explained as the result of an unprecedented peak of C, especially Infant C.

Chapter seven further develops the biohistory model by addressing events in England, Europe and Japan. The analysis indicates that a rise in C is driven by high V resulting in a high level of stress, which reached a peak in the sixteenth century. The subsequent decline in V and stress eventually allows C to fall. This is called the “civilization cycle.”

Chapter eight explores how population fluctuations in species such as lemmings and muskrats can be explained by changes in C and V. These “lemming cycles” are used to explain patterns such as the decline of Chinese dynasties, the virulence of the Black Death in medieval Europe, the timing of the Renaissance, and conflicts such as the Wars of the Roses.

Chapter nine looks at wars and revolutions that follow peaks of population growth and/or the end of previous wars. These are explained as a consequence of larger families and anxious mothers causing an increase in V in an age cohort. When males reach their early twenties their greater aggressiveness has a disproportionate influence on society and makes it easier for governments to engage in war. Findings are used to explain both the cause and timing of the French Revolution, the First and Second World Wars in Europe, the Japanese attack on Pearl Harbor, the Chinese Cultural Revolution, and the more aggressive attitudes of Iranians in recent years.

Chapter ten addresses the decline and fall of civilizations. C promotes larger states and more advanced economies, while V promotes higher birthrates and martial vigor. Civilizations collapse because declining V causes military weakness, and declining C causes political weakness and economic decay.

Chapter eleven analyses the rise and fall of Rome. Roman civilization was the result of an unprecedented rise in Infant C, driven by cultural systems imported from the Middle East. V and stress among the Romans appear to have peaked in the sixth century BC, while C peaked around 250 BC and was followed by a prolonged decline in both C and V. The fall of C explains the change from Republic to Empire and the subsequent collapse.

Chapters twelve and thirteen focus on why some societies are less vulnerable to the loss of V and C and thus become more durable. This is attributed to the presence of a stability factor known as “S” which leads people to indulge infants yet be stricter with older children. S reduces the unstable infant C and increases child V, making the society more conservative. Increased S is likely due to genetic change that arises from the experience of civilization, especially civilization collapse, which confers a demographic advantage on people with higher S and renders future collapse less serious and prolonged. The rise of S is traced in China and India.

Chapter fourteen traces the rise of S in the Middle East, from the low S Sumerians to the higher S empires of later times. Civilized societies developed high C cultural systems, while their “barbarian” neighbors had higher V because of harsh living conditions. The civilized peoples transmitted higher C cultures to the barbarians, who transmitted higher V to the settled lands by immigration and conquest. A gradual rise in both C and V culminated in the Arab conquest and the rise of Islam, seen as an especially powerful and durable cultural system which promotes long-term success at the expense of economic progress. A clear implication is that the Muslim populations of the Middle East will spread and gradually assimilate most of the world into their own faith and culture, beginning with Europe. Patriarchy and purdah, not liberal democracy, will be the true “end of history.”

Chapter fifteen approaches the most pressing issue in this book—the decline of Western civilization. Changes in Western countries over the past 150 years, and especially since the 1960s, are the result of a dramatic fall in both C and V. Evidence of falling C includes the declining age of puberty, increased sexual freedom, reduced control of children, declining work ethic, and economic stagnation. Signs of falling V include female emancipation, plunging birth rates, and a reduced enthusiasm for war. Though not all of these are negative, the end result must be economic decline and political collapse. Knowledge of the underlying biology indicates that no conventional social or political policy can reverse the process.

The model in this book presents our current understanding of the topics addressed. There will of course be additions and amendments as a result of further research and testing. Selected proposals are described in a final section.

This book is intended as a companion volume to *Biohistory: Decline and Fall of the West.*[2] It contains fuller evidence and the references not included in what is intended to be a shorter, more popular work. So that readers may easily cross from one version to another, the chapter structure remains the same. For example, anyone wanting more information about war than contained in chapter nine of the popular work may open chapter nine of this version and find further examples and longer descriptions. The shorter version also contains substantial material not included in this version, including different quotations and illustrations, but either book will give the reader a comprehensive understanding of biohistory.

[2] J. Penman, *Biohistory: Decline and Fall of the West* (Newcastle: Cambridge Scholars Publishing, 2014).

CHAPTER ONE

OF SCIENCE AND TEMPERAMENT

A key purpose of this book is to explain why some human societies have developed civilizations and others have not. For example, what differentiates humans who practice agriculture and form large-scale political and economic systems from those that live as hunter-gatherers in small bands? Why do the power and affluence of civilizations change so much and so quickly, with large, stable societies dissolving into anarchy, and others growing rapidly in influence and wealth?

Historians, archaeologists and economists have sought to understand these changes by looking at economic pressures, population growth, warfare, environmental change and the actions of charismatic leaders. Biohistory uses a different approach. It starts with the premise that humans are biological beings and therefore influenced by the same basic principles that affect our close non-human relatives. Genetically speaking we are very similar to other mammals. We share 95–98% of our genes with chimpanzees and, according to the latest results from Celera Genomics, about 85% with mice.[3]

There are many forms of behavior unique to humans. Apart from ants and termites, no other species unites thousands of individuals to work together and fight against outsiders. No other species develops market economies, uses money, builds machinery, establishes religions and formal codes of morality, or wears clothing by choice.

But in terms of family and social patterns, human behavior is less distinct. We control or punish our offspring, neglect them or provide intensive care. We can be monogamous, polygynous or promiscuous, and our levels of sexual activity vary enormously. We may mate immediately after puberty or delay breeding for a decade or more. Males can be dominant over females or vice versa. Societies can be egalitarian or hierarchical. We can work hard, even in the absence of real need, or lie back and take it easy. We can be aggressive or peaceful, angry or affectionate, suspicious or trusting. Every one of these behaviors has a direct equivalent in terms of animal behavior, as described later in this chapter.

Cross-cultural evidence

But the interesting point is that certain family and social behaviors are more often found in large-scale civilizations with complex economies. As detailed in the following chapters, ethnographic studies indicate that people living in long-civilized societies are more likely than those in pre-literate societies to restrict sexual activity, marry later, form monogamous nuclear families, and control their children's behavior. The extremes of such behavior can be found in northern Europe during the nineteenth century, when children were rigorously controlled from infancy and sexual behavior was strictly limited—especially for women. But similar patterns can be seen in other parts of the world.[4]

Biohistory proposes that there is an underlying *temperamental* difference between civilized and non-civilized societies, expressed to some extent in these family and personal behaviors but also in attitudes towards political authority and the market. In this and future chapters we will see that this temperamental difference can be explained in physiological terms. It will also be proposed that it is the development of this "civilized" temperament that makes civilization possible, whereas the loss of it is followed by a weakening and eventual collapse of the society affected. The best-known example is the decline and fall of the Roman Empire. Consider some of this evidence.

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[3] The more commonly used figure is 98%, but recent analysis suggests 95% might be more meaningful. R. J. Britten, "Divergence between Samples of Chimpanzee and Human DNA Sequences is 5%, Counting Indels," *Proceedings of the National Academy of Science U.S.A.* 99 (21) (2002): 13633–5; E. R. Winstead, "Humans and Mice Together at Last," *Genome News Network* (May 31, 2002).

[4] Historical studies provide a more mixed picture, with extended families and very early marriage evident in areas such as Eastern Europe and Asia. But since this evidence largely deals with elite families it is not clear how typical they are of the general population. Recent ethnographic studies, dealing with non-elite families and using precise quantitative measures, tend to show the differences indicated.

First, as long ago as the 1930s, J. D. Unwin found that civilized societies are more likely to control sexual behavior, a finding confirmed by later cross-cultural studies.[5] Related studies have found that societies with severe obedience training are more politically complex and more likely to be farmers and herders than hunters or fishers.[6]

These studies are meticulous and well researched, but from the viewpoint of biohistory they have significant problems. The first is that, apart from Unwin, they tend to exclude the societies with the biggest states and most advanced economies such as those of India, China, Europe and the Middle East, which show the most extreme forms of these behaviors.

Second, in terms of parental behavior these studies focus on the *aim* of control or punishment, such as to promote obedience or sharing. This is thinking in rational terms—that someone taught to be obedient will more likely obey others as he or she grows up. But in biological terms what is far more important is the *level* of control or punishment. For example, a severe punishment increases the level of stress hormones such as cortisol, whether the punishment is for disobedience, breaking cultural taboos or merely because the parent is bad-tempered. Similarly, we will see that it is the level of control that matters more than the purpose of the control. Both punishment and control have profound effects on hormones, on epigenetics (the way in which certain genes are switched on and off), and thus on adult temperament and behavior.[7]

Third, most studies fail to distinguish between control and punishment, using terms such as "severity of obedience socialization" which include both. In biochemical and behavioral terms, control and punishment have very different effects.

Finally, they do not always distinguish the age at which training applies. In later chapters evidence is presented from rat and monkey experiments showing that the same influence at different ages can have different or even opposite effects. The key distinction is between infancy, when mammals are nursed by their mother, and the juvenile period before puberty. In humans these ages are roughly 0–2 and 6–12.

The Cross-cultural survey

To better understand the family and social patterns linked to civilization, a study of 67 societies was made, ranging from hunter-gatherers to the long-civilized peoples of Europe and Asia. As with other cross-cultural studies, information from ethnographic studies provided quantitative scores for political, economic, family and childrearing variables. The ethnographies chosen were those with relatively detailed information on childrearing patterns. Full details of the study are given at www.biohistory.org.

The first point to note is that the findings of earlier studies linking controls on sexual behavior to measures of political and economic complexity are verified (see Table 1.1 below).

Table 1.1. Correlations between political and economic complexity and limits on sexual behavior.[8] Societies which restrict sexual behavior are more likely to be politically complex and with advanced economies. For example, the size of political units is positively correlated with restrictions on premarital sex.

	Premarital sex restricted	Adultery restricted	Divorce restricted
Size of political unit	.53**	.51**	.35*
Hereditary status	.39**	.43**	.41
Market economy	.45*	.54*	
Status from wealth versus generosity	.46*	.47*	.30

[5] J. D. Unwin, *Sex and Culture* (Oxford: Oxford University Press, 1934), 13–14, 27–9, 315–7, 321; W. N. Stephens, *The Family in Cross-cultural Perspective* (New York: Holt, Rinehart & Winston, 1963), 256–258.
[6] F. B. Aberle, "Culture and Socialization," in *Psychological Anthropology*, edited by F. L. K. Hsu, 386 (Homewood, Illinois: Dorsey Press, 1961); R. Barry, I. Child & M. K. Bacon, "Relation of Child Training to Subsistence Economy," in *American Anthropologist* 61 (1959): 56–60.
[7] Guy Riddehough & Laura M. Zahn, "What is Epigenetics" *Science* 330, (October 2010), http://www.sciencemag.org/content/330/6004.toc (accessed 13 September 2014).
[8] A full account of the coding system, codes for each society and significant correlations are given at www.biohistory.org.

Routine work	.42**	.48**	
Deities enforce morality	.30*	.30*	
Modesty in dress	.51**	.53**	
significance	**.001	* .01	Others: .05

Societies which insist on premarital chastity, sanction adultery and restrict divorce are more likely to form large political units, have market economies, work at routine jobs such as farming, and strive to achieve individual wealth. Their religious systems more often include moral codes.

Table 1.2 shows that societies which are politically and economically complex also have distinct family patterns. Compared with small-scale societies they are more likely to form nuclear monogamous families, marry late and control their children's behavior.

Table 1.2. Correlations of political and economic variables with family and social variables.[9] Societies which are politically and economically complex are more likely to form nuclear monogamous families, marry late and control their children's behavior.

	Premarital sex restricted	Monogamy versus polygyny	Nuclear family	Marry late	Control children	Children wanted
Size of political unit	.53**	.52**	.46**	.51**	.56**	.28*
Hereditary status	.39**	.42**		.55**	.50**	.31
Market economy	.45*	.43**	.45**	.39*	.59**	.28
Status from wealth vs generosity	.46*	.41**	.65**	.42*	.56**	
Routine work	.42**	.51**	.35*	.41**	.58**	
Deities enforce morality	.30*		.42**	.30	.51**	.38
Modesty in dress	.51**	.62**	.54**	.54**	.68**	.25
significance	**.001	* .01	Others:	.05		

These variables also correlate strongly with each other, as shown in Table 1.3 below.

Table 1.3. Significant Correlations among family and social variables linked to civilization.[10] Patterns of family behavior found in more complex societies, such as monogamous nuclear families, late marriage and control of children, correlate independently with each other.

	Monogamy versus polygyny	Nuclear family	Marry late	Control children	Children wanted
Premarital sex restricted	.48**	.30*	.43**	.38**	.32*
Monogamy vs polygyny		.30	.50**	.36*	
Nuclear family			.29	.33*	
Marry late				.54**	

[9] See www.biohistory.org

[10] See www.biohistory.org.

Control children					.31*
significance	**.001	* .01	Others:	.05	

Table 1.4 below shows that measures of political and economic complexity correlate strongly. Note the link to modesty in dress, which has no obvious connection with other features of civilization.

Table 1.4. Correlations among measures of political and economic complexity.[11] Politically complex societies tend to have advanced economies and to be modest in dress.

	Hereditary status	Market economy	Status wealth	Routine work	Deities moral	Modest dress
Size of political unit	.58**	.62**	.61**	.47**	.47**	.69**
Hereditary status		.39**	.45**	.34*	.28	.48**
Market economy			.49**	.55*	.41**	.62**
Status from wealth				.38**	.39**	.69**
Routine work					.22	.57**
Deities enforce morality						.39*
significance	**.001	* .01	Others:	.05		

It is no surprise that politically complex societies should have more advanced economies. What is interesting is that they are just as likely to insist on premarital chastity and control children. In other words, limits on sexual behavior and control of children are just as distinctive a feature of larger states as markets. It is logical that larger states should have market economies, if only because political union makes trade easier, but why should they limit sexual behavior or control their children?

This link is not without exceptions, of course. There are societies combining advanced political and economic systems with liberal standards of sexual behavior. The modern West and late Republican Rome are two obvious examples, which will become highly significant once we understand *why* civilized societies restrict sexual behavior. These apparent exceptions will then help us to understand why civilizations fall.

The temperamental basis of civilization

What is needed is an explanation of why certain behaviors such as sexual restraint are more prevalent in civilized societies. Biohistory proposes that they represent underlying biological systems that adjust people's temperaments to the needs of civilization. This makes them more accepting of wider political authority, more inclined to perform routine work, better suited to a market economy, and more accepting of impersonal moral codes such as those taught by religious systems. They also change their behavior in other ways, such as increasing modesty in dress and reducing tolerance of pre-marital sex.

The next step is to explore the implications of these behaviors. A core theme of biohistory is that humans are in many ways similar to animals, sharing up to 95% of our genes with other species. Thus it is that the family and personal behavior associated with civilized societies can also be observed in animals. Primates in particular can delay breeding, the equivalent of premarital chastity and late marriage. They can form nuclear monogamous families, and they can control the behavior and movements of their offspring. But which species are more likely to show such behaviors, and in what circumstances?

Gibbons and baboons

The study begins with two primate groups: gibbons and savannah baboons, which display extremes of these behaviors. Gibbons, a tree dwelling ape living in the forests of South-East Asia, act more like civilized peoples. Baboons, a largely terrestrial monkey living in the open grasslands of Africa, act more like the people of small-scale societies.

For example, gibbon are far less sexually active than baboons. They are also less sociable. Studies of three different populations show that they spend only 6%, 4% and 1.3% of the day in social activities.[12] By comparison, studies of 18 baboon populations show that they spent an average of 11.9% of their day in social

[11] www.biohistory.org.

[12] S. M. Cheyne, "Behavioural Ecology of Gibbons (Hylobates albibarbis) in a Degraded Peat-Swamp Forest," *Indonesian Primates: Developments in Primatology: Progress and Reports* (2010): 121–56.

activities, ranging from a low of 4.5% to a high of 22.7%.[13]

Gibbons are not only less social but also less tolerant of each other than baboons, and indeed of most primates. Males usually drive away other adult males, and females will not tolerate other females, including their own offspring after they reach puberty. Mated pairs defend territories, which represents an extreme in social intolerance. They do not totally avoid other gibbons, as they have been observed grooming and playing with individuals from neighboring territories.[14] But the only instance in which individuals of the same gender *share* a territory is when two males bond with a single female, a pattern rare in primate societies but forming 15% of families in one well-studied population.[15] In other cases, gibbons typically form nuclear monogamous families.

Among baboons, by comparison, no monogamous or polyandrous population has ever been found. Baboon troops normally consist of multiple males and females, although troops in some areas may have a single male with multiple females. One study comparing 23 populations found an average group size of 67, ranging from a low of 19 to a high of 247.[16] In these troops, the dominant male tends to monopolize females in estrus and sire most of the young, with other males having access only when the dominant male is distracted.[17] In human terms, baboons are promiscuous or in some cases polygynous, but never monogamous.

Gibbon populations tend to be limited in size by restricted breeding. Mating is delayed until after animals establish a territory. One study found that this did not happen until around the age of 10, two years after gibbons reach full adult size and several years after sexual maturity.[18] For this and other reasons, gibbons reproduce below their potential reproductive rate. For example, a study of 7 gibbon females over a 6-year period found that only one gave birth more than once, two failed to breed at all, one remained unpaired, and the seventh female lost her mate to another female. This is the non-human equivalent of late marriage and limited sexual activity.

By contrast, baboon populations appear to be limited mainly by predation and infanticide. Females are sexually active soon after puberty and males whenever they can be.

A related difference is that gibbons are highly discriminating in their choice of mates. While different species are fertile with each other and their ranges often overlap, only occasionally do they interbreed in the wild. They can distinguish even closely related species living in the same area by the sound of their calls, which are thought to be important in the maintenance of pair bonds.[19] Efforts to breed gibbons in captivity result in only half the presented mates being accepted, even when no other mate is available.[20]

Baboons, on the other hand, seem to be far less picky. A male baboon will mate with any fully mature female in estrus. Females also appear to be less discriminating because they solicit mating from around ten days before ovulation, even though only juveniles and adolescents are interested at such times.[21]

There are no direct observations of parental control among gibbons, but parents stay in close and continuous contact with their young until the age of puberty. Baboon mothers, by contrast, wean their young early and cease

[13] D. L. Cheney & R. M. Seyfarth, *Baboon Metaphysics: The Evolution of a Social Mind* (Chicago: University of Chicago Press, 2007).
[14] T. Q. Bartlett, "Intragroup and Intergroup Social Interactions in White-Handed Gibbons," *International Journal of Primatology* 24 (2) (2003): 239–59; U. Reichhard & V. Sommer, "Group Encounters in Wild Gibbons (Hylobates lar): Agonism, Affiliation, and the Concept of Infanticide," *Behaviour* (1997): 1135–74.
[15] W. Y. Brockelman, U. Reichhard, U. Treesucon & J. J. Raemaekers, "Dispersal, Pair Formation and Social Structure in Gibbons (Hylobates lar)," *Behavioral Ecology and Sociobiology* 42 (5) (1998): 329–39; T. Savini, C. Boesch & U. H. Reichhard, "Varying Ecological Quality Influences the Probability of Polyandry in White-Handed Gibbons (Hylobates lar) in Thailand," *Biotropica* 41(4) (2009): 503–13; V Sommer & U. Reichhard, “Rethinking Monogamy: The Gibbon Case,” in *Primate males: Causes and Consequences of Variation in Group Composition*, edited by P. M. Kappeler (Cambridge: Cambridge University Press, 2000); U. Reichhard, "The Social Organization and Mating System of Khao Yai White-Handed Gibbons: 1992–2006, " *The Gibbons* (2009): 347–84.
[16] D. L. Cheney & R. M. Seyfarth, *Baboon Metaphysics: The Evolution of a Social Mind* (Chicago, University of Chicago Press, 2007).
[17] S. C. Alberts, J. C. Buchan & J. Altmann, "Sexual Selection in Wild Baboons: From Mating Opportunities to Paternity Success," *Animal Behaviour* 72 (5) (2006): 1177–96.
[18] Brockelman et al., "Dispersal, pair formation and social structure in gibbons," 329–39; T. Geissmann, "Reassessment of Age of Sexual Maturity in Gibbons (Hylobates spp.)," *American Journal of Primatology* 23 (1) (1991): 11–22.

[19] J. C. Mitani, "Species Discrimination of Male Song in Gibbons," *American Journal of Primatology* 13 (4) (1987): 413–23.
[20] A. W. Breznock, J. B. Harrold & T. G. Kawakami, "Successful Breeding of the Laboratory-Housed Gibbon (Hylobates lar)," *Laboratory Animal Science* 27 (2) (1977): 222–8.
[21] Cheney et al., *Baboon Metaphysics*.

to provide much care thereafter. Gibbons also spend far more time foraging for food than do baboons. Their food is widely scattered and generally in small quantities, so only constant movement and searching can provide enough food to survive. This is the non-human equivalent of very hard work.

Limited food as an explanation for gibbon behavior

These differences can be explained by one simple observation—gibbons are far more likely to be short of food.[22] They live in one of the most food-restricted environments on Earth—the tropical forests of south-east Asia. Typically, tropical forests are lush and productive with a wide variety of plants, including fruiting trees. If one plant species is not productive, another is likely to be. But there are major problems—many leaves and fruit contain dangerous toxins, and forest primates tend to be very selective feeders. Only the fruit or leaves of particular trees at certain stages of ripeness are suitable. Favored food plants are also widely scattered, so that forest-living primates such as gibbons must spend a great deal of their time foraging.

Another factor in gibbon behavior is that food supplies, though restricted, are relatively constant throughout the year. There are variations in the availability of certain foods, so the type of food taken will differ from season to season, but the sheer number of plant species means that there is always something to feed on however difficult it may be to find.[23]

In such conditions gibbon numbers grow to the absolute limit allowed by the forest larder. Hunger is thus likely to be a daily rather than yearly problem.[24] A further factor is that trees make gibbons less vulnerable to predation, so populations are limited primarily by the carrying capacity of the environment.[25]

Other evidence is consistent with this shortage of food. In Malaysia, for example, gibbons survive only below 500 meters. This is not because of predation or competition from other species, but rather because any significant reduction in food quality or increased effort involved in traveling put their energy budget in the red. In other words, food is so hard to find that a gibbon can barely find enough to maintain itself, even with an exclusive territory. Nursing mothers have been seen in notably poor condition. Intra-group squabbling over food is common and may account for why the young are expelled from their group. Some gibbon species are found at slightly higher altitudes, but even with these there is often too little food to survive.[26] One study found significantly higher rates of juvenile mortality among gibbons where home ranges were larger and animals had to travel further in search of food.[27]

Baboons, on the other hand, tend to live in environments where food supplies are highly variable. Through much of the year and even (in some areas) for several years in a row, food may be plentiful. But during times of drought it can be very scarce, resulting in severe stress and even starvation.[28] This environment is associated with a different set of behavioral responses.

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[22] Monogamy is commonly found in species with limited food and the consequent need for females to defend an exclusive territory, though there is an alternative explanation in terms of avoiding infanticide by males. C. Gelling, "Evolution of Mammalian Monogamy Remains Mysterious," *Science News* August 2, 2013. https://www.sciencenews.org/article/evolution-mammalian-monogamy-remains-mysterious.

[23] P. Fan, Q. Ni, G. Sun, B. Huan & X. Jiang, "Gibbons under Seasonal Stress; the Diet of the Black Crested Gibbon (Nomascus concolor) on Mt. Wuliang, Central Yunnan, China," *Primates* 50 (1) (2009): 37–44.

[24] L. A. Isbell, "Predation on Primates: Ecological Patterns and Evolutionary Consequences," *Evolutionary Anthropology Issues, News and Reviews* 3 (2) (1994): 63–4.

[25] D. F. Makin, H. F. P. Payne, G. I. H. Kerley & A. M. Shrader, "Foraging in a 3-D World: How does Predation Risk Affect Space use of Vervet Monkeys?" *Journal of Mammalogy* 93 (2) (2012): 424–7.

[26] J. O. Caldecott, "Habitat Quality and Populations of two Sympatric Gibbons (Hylobatidae) on a Mountain in Malaya," *Folia Primatologica* 33(1980): 291–309.

[27] T. Savini, C. Boesch & U. H. Reichhard, "Home-Range Characteristics and the Influence of Seasonality on Female Reproduction in White-Handed Gibbons (Hylobates lar) at Khao Yai National Park, Thailand," *American Journal of Physical Anthropology* 135 (1) (2008): 1–12.

[28] W. J. Hamilton, "Demographic Consequences of a Food and Water Shortage to Desert Chacma Baboons, Papio ursinus," *International Journal of Primatology* 6 (5) (1985): 451–62; Cheney et al., *Baboon Metaphysics*. L. R. Gesquiere, M. Khan, L. Shek, T. L. Wango, E. O. Wango, S. C. Alberts & J. Altmann, "Coping with a Challenging Environment: Effects of Season Variability and Reproductive Status on Glucocorticoid Concentrations of Female Baboons (Papio cynocephalus)," *Hormones and Behaviour* 54 (3) (2008): 410–6; S. C. Alberts & J. Altmann, "The Evolutionary Past and the Research Future: Environmental Variation and Life History Flexibility in a Primate Lineage," *Developments in Primatology: Progress and Prospects Part II* (2006): 277–303; D. K. Brockman & C. P. van Schaik, *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (Cambridge: Cambridge University Press, 2005), 159.

The advantages of different behavior in different environments

Primatologists consider troop size to be a trade-off between foraging efficiency and defense against predators. Feeding in large groups is inefficient. If food supplies are scarce or scattered in small patches, a great deal of time must be spent in searching for nutrients. A patch that would feed an individual for an hour might feed a larger group for only minutes. Socializing is an unnecessary distraction from time spent searching for food or resting, and relatively infrequent socializing is a trade mark of groups when food is scarce.

But if food is plentiful or in large patches, either because the land is productive or because there are many deaths from predation or occasional famine, then larger groups are better. More animals are available to provide warning against predators, or even to attack them.[29] Larger groups may also provide defense against competing groups of the same species. For example, in one study of three baboons baboon troops impacted by a drought, the smallest troop was driven from the most productive area so that its numbers dropped by three quarters. Meanwhile, the larger groups maintained or even increased their numbers.[30] When large groups are advantageous, socializing becomes a valuable way of cementing social ties and holding the group together. This is the same benefit we saw from socializing in hunter-gatherer bands.

An example of the trade-off between food supply and group size can be seen in a study of baboon troops in Amboseli National Park, where groups ranged in size from 8 to 44 members.[31] Baboons in the smallest troop obtained the same energy intake while spending half as much time foraging as those in the largest troop. However, they were observed spending more time near trees and were more likely to choose an elevated spot for resting, indicating a greater caution about predators. In a Botswana baboon population studied intensively over ten years, deaths from predation were greatest during the floods, when troop members were scattered and less able to warn other members of predators.[32]

On the other hand, gibbons are rarely taken by predators because of their agility and the time spent high in the forest canopy.[33] On average, gibbon populations contain a relatively high proportion of adults, indicating both low mortality and low birth rate.[34] In their environment, having too many young could be a disaster. Pregnancy is a highly demanding state when food is in short supply. Young that are born in less than optimal conditions are unlikely to survive, and those that do will be weak and unable to compete. Thus the best strategy is to limit breeding by delaying puberty and limiting sexual activity. Territory is also a factor. Normally, gibbons will not breed if unable to command an exclusive territory that can feed the mated pair and their young. Without such a territory, a pregnancy is unlikely to produce successful young and could put the female's life at risk. Given that death from predation is rare, it is far more sensible to wait for a suitable territory to become available.

Environmental constraints also govern reaction to predators. Gibbons are timid about predators, fleeing through the treetops at any sign of disturbance. Generally, baboons are far bolder, though the actual response depends on the predator. For lions, against which they have no defense, they can only be vigilant, giving alarm calls and hiding in trees. But for leopards:

> [If] the baboons are able to isolate a leopard in a bush, tree, or aardvark hole, they immediately surround it, screaming, alarm-calling, and lunging at it, seemingly without fear. Although male baboons, with their size and enormous canines, are much better equipped than females to fight a leopard, the mass mobbing involves baboons of every age and sex. Juveniles, adult females, even mothers with young infants join to form a huge, hostile mob that tries to corner the leopard. The attack continues even after some baboons have received slashes on their arms, legs, and face that open up huge wounds.[35]

Leopards are not uncommonly killed by such attacks.

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[29] Cheney et al., *Baboon Metaphysics*.
[30] C. Brain, "Deaths in a Desert Baboon Troop," *International Journal of Primatology* 13 (6) (1992): 593–99.
[31] P. B. Stacey, "Group Size and Foraging Efficiency in Yellow Baboons," *Behavioral Ecology and Sociobiology* 18 (3) (1986): 175–87.
[32] Cheney, *Baboon Metaphysics*.
[33] U. Reichhard, "Social Monogamy in Gibbons: The Male Perspective," in *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, edited by U. Reichhard & C. Boesch (Cambridge: Cambridge University Press, 2003), 192; N. L. Uhde & V. Sommer, "Antipredator Behavior in Gibbons (Hylobates lar, Khao Yai/Thailand)," in *Eat or be Eaten: Predator Sensitive Foraging among Primates*, edited by L. E. Miller (Cambridge: Cambridge University Press, 2002).
[34] Mitani, "Species Discrimination of Male Song in Gibbons."; T. Geissmann, "Inheritance of Song Parameters in the Gibbon Song, Analysed in 2 Hybrid Gibbons (Hylobates pileatus X H. lar)," *Folia Primatologica* 42 (1984): 216–35.
[35] Cheney et al., *Baboon Metaphysics*.

More abundant food makes animals bolder and more group-minded but does not fully account for the level of aggression found in savannah baboons. Aggression is part of a complex of social traits which will be discussed in chapter four.

Paradoxically, timidity makes sense when the risk of predation is low. Warning of a predator is dangerous and mobbing it far more so. Thus, there is less point in doing it when escape is easy. But when the predator is likely to make a kill, attempting to discourage or even kill it may be worth the risk of confrontation.

Not only are gibbons, with their arboreal habitats, less vulnerable to predators, they are also remarkably long-lived and have been known to reach 44 years in captivity.[36] Baboons are much shorter-lived. Female baboons may live to more than 20 years if not taken by a predator, but the life of male baboons could be described as "nasty, brutish and short." Fierce battles for dominance, together with predation, mean most never reach this age.[37] Even in captivity baboons rarely live beyond the age of 30.[38] This is especially striking since larger animals typically live longer, and gibbons are half or less the weight of baboons.[39]

Both longer *and* shorter lives aid survival and success. If premature death is unlikely, as for gibbons, the most successful animals are those which can maintain their bodies and wait for better times. But if death can happen at any moment, as among baboons, the best strategy is to put maximum effort into breeding fast, even if it often shortens life. In one Botswana baboon population most deaths among adult females and juveniles were due to predation, causing up to 95% of adult female deaths. In a single year, 25% of the troop's adult females disappeared from confirmed or suspected predation.[40] To maximize offspring a female must breed as fast as possible, because she may not be around next year.

This applies even more to males, since dominant males tend to sire most of the young. Fierce competition for dominance and the consequent breeding rights mean that male baboons often die from wounds sustained during fights.[41] So when predation is high the advantage shifts from long-term survival to faster breeding.

A similar argument applies to choice of mates. It makes sense that animals in food-limited environments should choose mates similar to themselves. Success in a stable, competitive environment means adapting to local conditions. An animal that does well in local conditions will reproduce most successfully with a mate that is similarly adapted, not one with variant genes that may be better suited to living somewhere else. Thus it is that gibbons have elaborate courtship rituals, so that subtle differences in behavior and appearance act to prevent interbreeding. Thus, regional populations become more distinct and eventually form a multiplicity of species, which is the case with gibbons.

By contrast, baboon environments are highly changeable so that having variant genes may be an advantage. Thus, baboons are far less discriminating and local sub-species readily interbreed, so that baboons are considered as a single species.[42]

Though there is no direct evidence that gibbons train or control their young, such behavior in a food-limited environment would make sense. Offspring are rare and vulnerable in a hungry world and need every care and protection if they are to survive. In particular they must learn which plants are good to eat and which are

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[36] Uhde et al., "Antipredator Behavior in Gibbons."
[37] Cheney et al., *Baboon Metaphysics*.
[38] L. D. Chen, R. S. Kushwaha, H. C. McGill, K. S. Rice & K. D. Carey, "Effect of naturally reduced ovarian function on plasma lipoprotein and 27-hydroxycholesterol levels in baboons (Papio sp.)," *Atherosclerosis* 136 (1) (1998): 89–98;
A. G. Comuzzie, S. A. Cole, L. Martin, K. D. Carey, M. C. Mahaney, J. Blangero & J. L. vandeBerg, "The Baboon as a Nonhuman Primate Model for the Study of the Genetics of Obesity," *Obesity Research* 11 (1) (2003): 75–80.
[39] Ma, S., Y. Wang & F. E. Poirier (1988). "Taxonomy, Distribution and Status of Gibbon (Hylobates) in Southern China and Adjacent Areas," *Primates* 29 (2): 277–86; A. H. Schultz, "The Relative Weight of the Testes in Primates," *The Anatomical Record* 72 (3) (1938): 387–94; R. W. Barton, D. G. Reynolds & K. G. Swan, "Mesenteric Circulatory Responses to Hemorrhagic Shock in the Baboon," *Annals of Surgical Innovation and Research* 175 (2) (1972): 204–9; N. J. Espat, J. C. Cendan, E. A. Beierle, T. A. Auffenberg, J. Rosenberg, D. Russell, J. S. Kenney, E. Fischer, W. Montegut, S. F. Lowry, E. M. Copeland III & L. L. Moldawer, "PEG-BP-30 Monotherapy Attenuates the Cytokine-Mediated Inflammatory Cascade in Baboon Escherichia Coli Septic Shock," *Journal of Surgical Research* 59 (1) (1995): 153–8.
[40] D. L. Cheney, R. M. Seyfarth, J. Fischer, J. Beehner, T. Bergman, S. E. Johnson, D. M. Kitchen, R. A. Palombit, D. Rendall & J. B. Silk, "Factors Affecting Reproduction and Mortality Among Baboons in the Okavango Delta, Botswana," *International Journal of Primatology* 25 (2) (2004): 401–28.
[41] Brain, C. (1992). "Deaths in a Desert Baboon Troop."
[42] R. I. M. Dunbar, "Time: A Hidden Constraint on the Behavioural Ecology of Baboons," *Behavioral Ecology and Sociobiology* 31 (1) (1992): 35–49; S. P. Henzi & L. Barrett, "The Historical Socioecology of Savannah Baboons (Papio hamadryas)," *Journal of Zoology (London)* 265 (3) (2005): 215–26.

poisonous and where they can be found.

Overall, gibbon behavior is an adaptation to chronic food shortage and low mortality, while baboon behavior is an adaption to normally plentiful food and high mortality.

Changes in behavior as a response to environment

While gibbon behavior is an adaptation to an environment with limited food, it is not a *response* to limited food. In a large number of studies no clear exception has been found to the common gibbon pattern of one male to one female (monogamy), with occasional families of two males to one female (polyandry). As has been mentioned, even in captivity where food is plentiful, gibbons are picky about mates and intolerant of their same-sex adult offspring.[43] Thus, gibbon behavior seems to be set by genes.

But this is not the case for many other species, including baboons and vervets—a small monkey native to southern and eastern Africa. Both baboons and vervets are found in a variety of habitats including mountain, desert, savannah, and dense forest, sometimes in the form of different sub-species. By their adaptability to a wide range of environments they differ from gibbons, which are only found in dense forest. And just as baboons and vervets can thrive in different environments, so they show a variety of social structures to suit different environments. None of these include monogamy with males and females paired, but the number of males in a troop can vary from one to many. Troops thus vary widely in size. And just as gibbons form small troops to adjust to a food-limited environments, baboons and vervets form smaller troops in marginal habitats with lower predation pressure. The link between behavior and environment is shown in Table 1.5 below, taken from a study of two populations of vervets in the wild—one in a productive swamp and the other in less productive dry woodland.[44]

Table 1.5 Ecological and demographic differences between two vervet groups[45]

	Dry Woodland	Swamp
Food quality	Lower	Higher
Water availability	Poor	Good
Group size	9–13	11–25
Average age of female at first birth (years)	5–6	4–5
Median interval between births (years)	2	1
Average infant mortality in first year	59%	57%
Predator sightings per hundred hours	4	6

The dry woodland population shows behavior associated with species in food-limited environments, such as gibbons. Troops are smaller and mothers gave birth later and less often, presumably allowing them to invest more in their young. This explains why the infant mortality rate is similar to that of the better-fed population, despite their poorer living conditions. Mothers did not spend more time with their young, but they were less likely to break contact and deny them their nipple. Predators were less of a factor, which is consistent with populations living near to the limits of its food supply.

It is not just the mother's behavior that increases care of the young in marginal habitats. A study of baboons showed that during seasons of food shortage the young were more likely to throw tantrums and thus achieve more attention and care from their mothers.[46]

It is an axiom of primate social behavior that groups of the same species are smaller in areas with scarcer food. As mentioned, the theory is that larger groups protect members against predators and provide an advantage in inter-troop competition. On the other hand, feeding is less efficient which reduces female reproductive rates and

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[43] B. L. Burns, H. M. Dooley & D. S. Judge, "Social Dynamics Modify Behavioural Development in Captive White-Cheeked (Nomascus leucogenys) and Silvery (Hylobates moloch) Gibbons," *Primates* 52 (3) (2011): 271–7.
[44] M. D. Hauser & L. A. Fairbanks, "Mother-Offspring Conflict in Vervet Monkeys: Variation in Response to Ecological Conditions," *Animal Behaviour* 36 (3) (1988): 802–13.
[45] Ibid.
[46] L. Barrett & S. Peter-Henzi, "Are Baboon Infants Sir Phillip Sydney's Offspring?" *Ethology* 106 (7) (2000): 645–58.

increases mortality from causes such as malnutrition or disease.[47] Smaller groups are more efficient for feeding purposes but provide less protection against predators and other troops.

For example, baboon populations in a marginal mountain area had smaller troops compared to those in a more food productive national park. Mothers also provided greater levels of care to their infants, with a longer interval between births. In turn, infant survival rates were actually better than in more typical baboon habitats with plentiful food.[48] These findings are consistent with the view that group size can be explained entirely in terms of feeding strategy. Troops of wide ranging sizes allocated similar amounts of time to foraging, in that they foraged with the same efficiency and travelled approximately the same distances to do so.[49] In terms of survival and success this is the optimum strategy because it permits animals to balance the advantages of smaller groups for effective foraging with the advantages of larger groups for mutual support and defense. On balance, group size among both baboons and vervets is a function of foraging efficiency, food availability and predator density.

Another difference is that, though animals in food-limited environments spend about the same time moving as animals in a more food abundant environment, they tend to travel a great deal faster. Baboon troops in areas with less than 700 mm of rain per year had a mean travel speed of around 2 km/hour, while those in areas with more than 1000 mm of rain travelled at an average of 0.5 km/hour.[50] When food is scarce and widely scattered, faster movement has clear advantages in terms of locating food and thus survival.

Many other studies have shown that primates in food-limited areas form smaller groups. For example, a study of Japanese macaques found that on an island where food quality was poor, the time animals spent on feeding was 1.7 times greater than on an island with better quality food. In the poor environment, monkeys also spent significantly less time grooming each other. There were fewer males in the groups but more solitary males outside of groups—an indication of social intolerance. These macaques were also more vigilant, even though there was far less aggression between groups.[51]

A further finding from this study is that males on the less productive island were never seen to mate with females in other groups or to transfer groups, a behavior common on the more productive island. This perhaps indicates a preference for mating with more similar and familiar animals, which is a feature of behavior in food limited environments.

All of these species seem to be genetically adapted to environments with more plentiful food, forming multi-male or one-male troops but not monogamous pairs. But there are other species which vary in behavior but with a bias towards food-limited patterns. Spider monkeys, which live in similar environments to gibbons, form gibbon-size groups when food is scarce but much larger ones in times of food abundance.[52]

The snub-nosed langur of Mentawai, a forested island off the coast of Sumatra, is one of the few primate species to be monogamous in its natural environment. Part of the island had been logged some ten years before the researchers arrived, and the forest regrowth provided ample food. The langurs in this area were more numerous than in the non-logged area and commonly formed larger troops with one male and multiple females. They were also bolder. Though hunted intensively by local people in both areas, those in the regrowth areas were noisier and less vigilant and thus more likely to be captured. People came from far afield to hunt them and rarely left

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47 C. P. van Schaik, "Why are Diurnal Primates Living in Groups?" *Behaviour* 87 (1/2) (1983): 120–44; C. A. Chapman, L. J. Chapman & R. W. Wrangham, "Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups," *Behavioral Ecology and Sociobiology* 36 (1) (1995): 59–70; C. Janson, "Aggressive Competition and Individual Food Consumption in Wild Brown Capuchin Monkeys (Cebus apella)," *Behavioral Ecology and Sociobiology* 18 (2) (1985): 125–38; G. Ramos-Fernández, D. Boyer & V. P. Gómez, "A Complex Social Structure with Fission–Fusion Properties can Emerge from a Simple Foraging Model," *Behavioral Ecology and Sociobiology* 60 (4) (2006): 536–49; Y. Takahata, S. Suzuki, N. Okayasu, H. Sugiura, H. Takahashi, J. Yamagiwa, K. Izawa, N. Agetsuma, D. Hill & C. Saito, "Does Troop Size of Wild Japanese Macaques Influence Birth Rate and Infant Mortality in the Absence of Predators?" *Primates* 39 (2) (1998): 245–51.

48 J. E. Lycett, S. P. Henzi & L. Barrett, "Maternal Investment in Mountain Baboons and the Hypothesis of Reduced Care," *Behavioral Ecology and Sociobiology* 42 (1) (1998): 49–56; S. P. Henzi, J. E. Lycett & S. E. Piper, "Fission and Troop Size in a Mountain Baboon Population," *Animal Behaviour* 53 (3) (1997): 525–35.

49 Lycett et al., "Maternal Investment in Mountain Baboons"; Henzi et al., "Fission and Troop Size."

50 Dunbar, "Time: A Hidden Constraint on the Behavioural Ecology of Baboons," 35–49.

51 C. Saito, S. Sato, S. Suzuki, H. Sugiura, N. Agetsuma, Y. Takahata, C. Sasaki, H. Takahashi, T. Tanaka & J. Yamagiwa, "Aggressive Intergroup Encounters in Two Populations of Japanese Macaques (Macaca fuscata)," *Primates* 39 (3) (1998): 303–12; N. Agetsuma & N. Nakagawa, "Effects of Habitat Differences on Feeding Behaviors of Japanese Monkeys: Comparison between Yakushima and Kinkazan," *Primates* 39 (3) (1998): 275–89.

52 D. Robbins, C. A. Chapman & R. W. Wrangham, "Group Size and Stability: Why do Gibbons and Spider Monkeys Differ?" *Primates* 32 (3) (1991): 301–5.

without an ample catch, whereas in the untouched forest they often ended up empty handed.[53]

It should be noted here that spider monkeys and langurs in larger troops exhibit the same boldness and large group dynamics but do not show the same levels of aggression found among large troops of baboons. Again, we will return to this important topic in chapter four.

The advantages of being able to change behavior as a response to changes in food

For species in environments where food availability varies there are benefits in being able to adapt behavior to different levels of food and predator threat, especially since the change in food supplies can happen very quickly. For example, snub-nosed monkeys in Yunnan form smaller groups during the winter when food is less available, and larger ones at other times of the year.[54]

When food is scarce and predators few, the best strategy is to spread out in smaller groups for more efficient feeding, travel faster in search of food, and spend less time in social activities such as grooming. And when predators are scarce, flight is a better response than dangerous practices such as mobbing. Mobbing is also less likely to be effective when groups are smaller.

The same argument applies to reproduction. When food is short, breeding rapidly and too early is a danger to mothers and offspring. It is far better to delay breeding until mothers are fully mature, and even then only when sufficient food is available. Births should be spaced and greater attention given to offspring to optimize their chance of survival. Ideally, individuals in such a group would spend less energy on fast reproduction and more on body maintenance and long-term survival.

When food is plentiful and predators are common, the opposite strategy is preferable. Coming together in large groups provides better defense against other groups and predators, to provide warnings or even attack them.

For optimum genetic advantage in food-affluent environments, breeding should start early because there is ample food for even immature females to rear their young. Birth intervals may be short and maternal care less intensive but the young will likely survive. Males should compete fiercely for reproduction, even at risk to their own lives, because they are unlikely to live very long as a result of predation.

We can also appreciate why animals in a food-limited environment, such as gibbons or monogamous langurs, should be more cautious about predators. When there are few dangerous predators, population rises to match the level of the food supply, so food becomes scarce. There is less point risking your life by mobbing a predator when it is unlikely to catch you. When predation is strong, however, population stays below the level supportable by the food supply, so food becomes relatively plentiful. Predators pose an extreme danger, so group size increases to allow for mutual warning and defense. In parallel, animals become bolder which allows for active mobbing.

The preceding points explain why Mentawaian langurs apparently acted contrary to their own survival interests, showing greater boldness in the productive areas where hunting was more prevalent. Plentiful food switches on the anti-predator response of larger and bolder troops, effective against snakes and eagles but not against men armed with shotguns.

There are studies documenting that food shortage is associated with the same behavioral response in humans as in non-human primates. In the cross-cultural survey, people who live in societies that are short of food are more monogamous and modest in dress than people in societies where food is plentiful. Women in these societies are also more likely to report that they do not enjoy sex (see Table 1.6 below).

Table 1.6. Behavior related to food shortage in the cross-cultural survey[55] Behaviors associated with food shortage in non-human primates are also more common in human societies reported as short of food.

	Shortage of food

[53] K. Watanabe, "Variation in Group Composition and Population Density of the Two Sympatric Mentawaian Leaf-Monkeys," *Primates* 22 (2) (1981): 145–60.
[54] B. Ren, D. Li, P. A. Garber & M. Li, "Fission–Fusion Behavior in Yunnan Snub-Nosed Monkeys (Rhinopithecus bieti) in Yunnan, China," *International Journal of Primatology* 33 (5) (2012): 1–14.
[55] See www.biohistory.org.

Divorce restricted	.25
Monogamy	.22
Women less interested in sex	.44
Modesty in dress	.37*
* .01 significance	Others: .05 significance

How do changed food conditions affect behavior?

Having identified the behavioral effects of food shortage, the next step is to identify how this comes about. Granted that it benefits individuals in times of food shortage to delay breeding or forming monogamous families, how could shortage of food give rise to such behavior? And why would it cause people to be modest in dress—something that has no parallel in animal behavior and yet, as we have seen, is strongly linked to other food-restricted behaviors (see Tables 1.1 and 1.2 above).

One hypothesis is that the primate groups become smaller in tougher conditions because animals have less time to service their social relationships. Another is that they split up because of competition for food.[56] Both of these ideas could be valid. Grooming plays a vital role in social cohesion, so animals that need to spend more time searching for food will have less energy for strengthening social bonds. And direct competition for food has a role in splitting groups, as we saw with gibbons. It is also not unreasonable that groups short of food should travel faster between feeding patches. But such explanations do not easily account for the full range of behavioral changes, such as why animals in food-limited environments flee from predators rather than mob them, breed more slowly, and give more attention to their young.

Biohistory proposes that the changes in behavior noted in tables 1.5 and 1.6 stem from a direct physiological response to hunger. This in turn has an epigenetic effect—hunger changes gene expression so that genes become more or less active.

Epigenetics is a relatively new field, but it has already led to powerful insights into the ways in which individuals develop. The key point is that animals which experience limited food availability, either because of a food-limited environment or reduced predator pressure, undergo physiological changes that alter their behavior. In effect, they behave more like gibbons and less like baboons. There are of course limits to this change. For example, the social behavior of baboons is far more flexible than that of gibbons, but no baboon groups have been found with the social organization of gibbons.

Note that a limited food supply or calorie restriction, which from now on will be identified as “CR,” does not mean starvation. Numerous studies have found that, short of malnutrition, CR has health benefits—limiting food intake delays aging and extends lifespan for many species, including primates. Other effects include reducing the likelihood of diabetes, cancer, cardiovascular disease and brain atrophy.[57] This reflects a shift of body resources from fast reproduction to body maintenance and longevity, responses that are optimal in environments with stable but limited food.

CR also appears to improve learning and memory—useful skills when locating scattered food resources in an environment such as a tropical forest. For example, a gibbon will be more likely to survive if it is good at remembering the location of a fruiting tree and how to reach it.

In chapter two we discuss evidence that hormone changes resulting from CR mediate the behavioral changes. Establishing this point is not easy in the wild, but a study of four vervet populations found that leptin levels were up to four times higher in the wet season, when food was more readily available (leptin is a hormone known to increase with plentiful food). And although female leptin levels varied widely depending on breeding conditions, and the other results were not entirely consistent, male leptin was lowest in the population with

56 Janson, "Aggressive Competition and Individual Food Consumption in Wild Brown Capuchin Monkeys,” 125–38; Chapman et al., "Ecological constraints on group size,” 59–70.

57 R. J. Colman, R. M. Anderson, S. C. Johnson, E. K. Kastman, K. J. Kosmatka, T. M. Beasley, D. B. Allison, C. Cruzen, H. A. Simmons, J. W. Kemnitz & R. Weindruch, "Caloric Restriction Delays Disease Onset and Mortality in Rhesus Monkeys," *Science* 325 (5937) (2009): 201–4.

lowest rainfall and smallest troop size.[58]

A recent study supplemented the diet of mice with minimal extra sugar, an amount equivalent to a human drinking three cans of soft drink a day. This is, in effect, a condition of super-abundant food, because of the high calorie content of sugar. The mice not only had a higher death rate than the mice which did not receive the supplement, but 26% fewer males were able to establish territories.[59] In other words, well-fed animals are less territorial.

The genetic and environmental components of CR behavior

The most successful species are those most well adapted in body and behavior to their environments. For example, gibbons are adapted to life in the rainforest in that their long arms are well suited to brachiating through the trees. A genetic predisposition to high CR behavior would similarly adapt their *behavior* to the tropical forest, where predation is low and population presses against the limits of the food supply. Adults would have to work hard to find food. They would have fewer young but spend more time looking after them so as to produce offspring that can flourish in their environment.

Baboons are adapted to life on the savannah and are far better than gibbons at moving along the ground. A genetic predisposition to low CR behavior would be adaptive to their environment where food is normally plentiful and breeding can occur early in the lives of females. They have no need to spread out or work overly hard to search for food. The threat of predators means they stand to gain from membership in larger troops, which provide many pairs of eyes to detect danger and contribute mutual defense. Larger groups also give them an advantage in competition with other troops. Further, if local food resources become limited, a larger group provides protection should it choose to migrate. A large, well-organized troop is better able to cope with the dangers of a strange environment than individuals or scattered nuclear families.

Such broad differences arise through the process of natural selection. When ancestral gibbons moved into the tropical forest, individuals with longer arms are likely to have found more food than those less capable of moving through the trees. Better-adapted animals would have more offspring carrying their genes which, over thousands of generations, would lead to their becoming the superb acrobats that we now observe. Similarly, in a resource-scarce environment, animals with CR genes would tend to be more reproductively successful in the sense that the survival rate of offspring would exceed that of animals such as baboons, despite producing fewer offspring in each generation. Such genes would also predominate in future generations.

Moving into an environment with more plentiful food, adaptation would work the other way. Genetically determined changes in patterns of sociability would accompany changes in sexual behavior and care of offspring. Behavioral changes would be hastened if all the CR systems operated as a single mechanism.

However, mammals have a faster (though not perfect) way of adapting to the environment than the slow process of natural selection. In the next chapter we discuss how the complex of behavior associated with rapid adaptation to changing food availability applies to other mammal species such as rats and mice. Within limits, what we as human beings have inherited is the capacity of individuals to change their level of CR-related behavior as a direct response to specific environmental conditions. The stimuli in this case are food-abundant and food-limited environments. The genetic code does not need to change for this process to work. The relevant genes can simply be switched on or off epigenetically via environmental triggers acting through hormones.

A clear implication of the preceding points is that the level of CR-related behavior is not always fixed or constant. Species adapted to a stable environment, such as gibbons, have minimal need to alter their behavior. But others, such as baboons and vervets, which inhabit multiple ecological niches, need to alter their CR-related behavior to suit. One can predict, therefore, that the greater the range of habitats, the more CR-related behaviors can change.

Such plasticity has its limits. Forest-dwelling species such as Mentawaian langurs vary between monogamous

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[58] P. L. Whitten & T. R. Turner, "Ecological and Reproductive Variance in Serum Leptin in Wild Vervet Monkeys," *American Journal of Physical Anthropology* 137 (2008): 441–8; N. Dracopoli, F. L. Brett, T. R. Turner & C. J. Jolly, "Patterns of Genetic Variability in the Serum Proteins of the Kenyan Vervet Monkey (Cercopithecus aethiops)," *American Journal of Physical Anthropology* 61 (1983): 39–49.

[59] J. S. Ruff., A. L. Suchy, S. A. Hugentobler, M. M. Sosa, B. L. Schwartz, L. C. Morrison, S. H. Gient, M. K. Shigenaga & W. K. Potts, "Human-Relevant Levels of Added Sugar Consumption Increase Female Mortality and Lower Male Fitness in Mice," *Nature Communications* 4 (2013): Article 2245.

and polygamous behaviors, while more open-country species such as baboons and vervets vary between multi-male and polygynous. This suggests that each species has a genetic "set point" for behavior that fits its most typical habitat, but that, within limits, behavior can vary as an adaptation to different habitats.

"Natural" levels of CR-related behavior in humans

Based on the observation of the behavior of current hunter-gatherers, whose subsistence patterns and social structures mirror those of our distant ancestors, the human set point for CR-related behavior appears to be low. Hunter-gatherers normally live in multi-family groups which travel and hunt together. For example, camps of the Mbuti pygmies consist of at least 6–7 families, the minimum required for the Mbuti practice of hunting with nets. Family groups move periodically and also change in composition as people attach themselves to different relatives by blood or marriage. The maximum size of such groups is determined by the needs of hunting. Too many people are seen as a disadvantage.[60] This pattern is nothing like that observed among gibbons and langurs where couples or polygynous males defend an exclusive patch of land. Subsistence patterns also have more in common with baboons than gibbons. Men spend much of their time hunting, which is far less routine than the intensive foraging of a rainforest primate. In this sense they also show no trace of CR-related behavior.

For human beings, having a low set point for CR-related behavior makes sense. Humans are physically adapted to life in the open, probably more so than baboons. Our efficient striding walk allows us to cover long distances in pursuit of prey, and compared with most primates we are poor at swinging through trees or even climbing them. Unable to outrun lions or leopards and poor at climbing trees, our ancestors suffered at the hands of numerous predators, which once again would make group defense and other low CR-related behaviors advantageous. This cluster of behaviors can be still be observed in group-living hunter-gatherers.

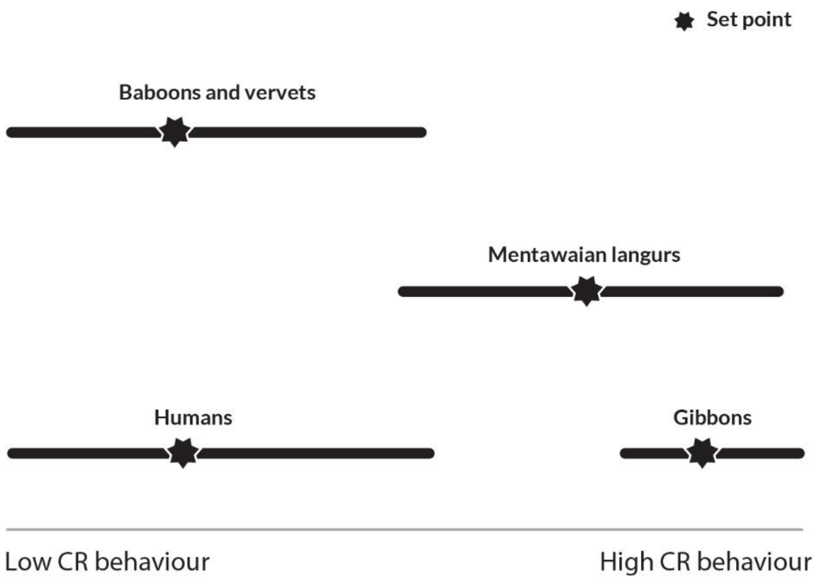
Like baboons and vervets, humans show a relatively large range of CR-related behavior. As mentioned earlier, civilized peoples tend to have very high levels. A farmer or factory worker usually lives with their spouse and dependent young on a defined plot of land (even if only an apartment), with most of their working hours spent on routine tasks. In this sense he acts more like a gibbon than a baboon or, in general terms, more like animals in a food-restricted environment.

However, unlike many nonhuman primate species, in no known human society do breeding couples defend their plots against all intruders, with each partner driving away visitors of the same sex. On the contrary, people in most societies tend to form pair bonds but are also highly cooperative. This behavior suggests the presence of a genetic bias towards monogamy, which takes a peculiar form. Instead of defending a territory, mated pairs have a strong and enduring bond within what (in primate terms) consists of a multi-male band. This applies to hunter-gatherers as much as farmers. In this we are unlike gibbons or langurs, because it permits us to form monogamous nuclear families even when CR-related behavior is only moderately high.

Still, the level of activation of the CR systems does determine the degree to which humans are faithfully monogamous. In some societies, such as Victorian Britain, monogamous norms were immensely strong, though even then not always observed. In other societies, such as in much of Africa, polygyny and even promiscuity are widely accepted. The level of CR-related behavior is indicated by the strength of the social forces requiring monogamy or permitting polygyny and/or promiscuity. So allowing for the fact that humans are more monogamous than many other primates, when their CR-related behavior is weak they are more likely to exercise polygynous and promiscuous behavior. Fig. 1.1 below depicts their overall CR-related behavior in a number of primate species, including humans.

[60] Turnbull, C. (1963) The Forest People, London, The Reprint Society, Pp 38-9

Fig. 1.1. Proposed set points and range of variation in CR-related behavior in various primates. Baboons and vervets are changeable but more likely to form multi-male bands. Langurs and gibbons are changeable but more likely to form single-male troops or even monogamous pairs. Gibbons are finely adapted to a food stable environment and thus less able to change behavior. Human hunter-gatherers are more like group-living baboons, with the exception of unusually strong pair bonds.



An obvious objection to this approach is that many civilized peoples today and in the recent past have relatively high levels of CR-related behavior without being short of food. For example, America in the nineteenth century had plentiful land and a fast-growing population, and yet was clearly high in CR-related behavior by human standards. This suggests that some factor other than food shortage was responsible for the behavior. To identify this factor or factors we must first study the biochemical and epigenetic effects of food shortage to gain an understanding of what CR-related behavior is really about.