Chapter 6
Mating Systems, Mate Choice, Marriage, Sexual Behavior, and Inbreeding

6.1 Introduction

There is a considerable body of research on the relationship between parasite stress and a range of values involved in human mate choice, romantic relationships, competition for mates, sexual behavior, and marriage systems. This chapter provides an overview of this fascinating and growing research area.

6.2 Polygyny

6.2.1 Low's Research

Bobbi Low (1988, 1990, 1994) did the earliest pioneering research connecting parasite stress with human marital relationships. She made an index of historical human parasite severity (the number of disease cases) comprised of seven major human disease categories, with parasite severity measured on a three-level scale that ranged from "disease absent" to "present and serious" to "widespread or endemic." Her three levels of parasite severity correspond to the three levels of parasite severity we used in our parasite severity measures made from the GLOBE data. (See, for example, Chap. 5 for discussion of the *Contemporary Parasite Severity* measure.) Her sample of human cultures was the 186 indigenous societies in the Standard Cross-Cultural Sample, a data set often used in cross-cultural anthropological research. The scores for the seven categories of parasites were summed for each society's geographic location leading to a parasite-severity variable that ranged from seven (corresponding to the situation where none of the parasites were present in a society's geographic range) to 21 (all seven parasite categories were endemic). She had multiple measures of polygyny across societies of the Standard Cross-Cultural Sample that had been reported already in the literature. All of the polygyny

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measures were intercorrelated and each reflects variation in the success of men in obtaining wives. Wife number for men ranged from zero to seven in the sample. (In this sample, there were no highly despotic indigenous societies, which, as shown by the historian Laura Betzig, are characterized by the huge number of wives and concubines obtained by a very small number of elite men (Betzig 1986)).

Low (1990) reported that, across the indigenous societies in the Standard Cross-Cultural Sample, parasite-severity scores are correlated positively with the degree of polygyny. Hence, as parasite severity increases across these societies, an increasingly small percentage of men monopolize more of the direct reproduction (offspring production) of women. As mentioned in Chap. 3, Low predicted this finding based on the parasite theory of sexual selection. Accordingly, among men, high parasite stress generates high variance in genetic and phenotypic quality, and thus it can be more adaptive for a woman to pair with a man who has a wife (or wives) than to engage in a monogamous marriage. Most men in these societies, however, are monogamously pair-bonded; only men of very high quality are polygynous. Such men provide high genetic quality to their offspring, plus resources that are attractive to women, even though the men are already paired with a mate(s). Typically, in these polygynous societies, female mate choice for marriage is a family affair (Chagnon 1992; Low 2000), so the decision of women to pair polygynously is not independent of the reproductive interests and decisions of the woman's family, especially the more influential and socially powerful male members of the family. Frank Marlowe (2003) tested the parasite-stress hypothesis of human polygyny by examining the subset of cultures in the Standard Cross-Cultural Sample that are foragers or hunter–gatherers, and repeated for this subsample Low's general finding across the entire sample.

6.2.2 Collectivisim and Polygyny

We hypothesize that collectivism is the value system that serves as a mediator of the relationship between the degree of polygyny and parasite stress. That is to say, collectivism is evoked by parasite adversity (as shown in Chap. 5) and hence is the value system that is a proximate cause of much of the polygyny in the ethnographic record of anthropology. We predict, therefore, that the degree of polygyny will correlate positively with the degree of collectivism across the societies in the Standard Cross-Cultural Sample. Our hypothesis is consistent with the greater role of the family in marriage arrangements under collectivism than under individualism (Buunk et al. 2010). Moreover, in-depth studies of modern polygynous households in the West (e.g., among Mormons) reveal highly collectivist values in those homes and in these polygynous communities in general (Hales 2007).

Pratto and Hegarty's (2000) research findings are consistent also with an important role of collectivism in promoting polygynous marriage systems. They studied among Western unmarried college students the relationship between social dominance orientation (SDO) and desire for multiple, simultaneous mating partners. SDO scores are correlated highly and positively with conservatism scores among

individuals (see Chap. 4). People with high SDO scores have an ideology that is more traditional than do people with low scores; this includes traditional values of social inequality, hierarchy, and sex roles, with male superiority and privilege. Pratto and Hegarty found that men scoring high on SDO were much more approving of polygynous sexual relationships (multiple female mates simultaneously) than were low-SDO-scoring men. The same pattern was not apparent among women—that is, women's SDO scores did not correspond to their approval of men having multiple, simultaneous mates. However, high SDO women, compared to low SDO women, placed more value on obtaining a high-status, high-earning mate. In sum, this research supports an abundance of other research, including that on family ties (discussed in Chap. 5), showing that conservatives prefer traditional values of family life; in particular, this study indicates that conservative women value resource-rich men to a greater degree than do individualistic (and thus more independent) or liberal women, and that conservative men have a greater passion for polygyny than liberal men do. The values of traditionalism and female dependency on a male pair-bond partner and simultaneity of mates of a man underlie polygynous marriage systems.

Male slave owners in the parasite-rich, collectivist Old South USA sometimes reproduced by polygyny despite monogamous marriage being the law of the land. Among historians, there are mixed opinions about the frequency of married slave owners fathering children by slaves, but, according to some accounts, male plantation masters oftentimes sired more children by slaves than by their legal wife (Betzig and Weber 1993). Van den Berghe's (1981) review of slavery systems, both in the South and in other parts of the world, led him to conclude that the mating system of the slave plantation, whenever and wherever it occurs, is polygyny. In regard to the pre-Civil War South, he points out that the owner, his sons, and overseers were paired and reproduced polygynously because "they had access not only to the white women whom they married—but also the pick of young slaves whom they took as concubines" (p. 132). He reports, too, that it was not until after the American Civil War and with Reconstruction that white men's access to African-American women was normatively and legally restricted.

6.3 Mate Choice

6.3.1 Gangestad and Buss' Research

Soon after Low's research linking marital polygyny and parasite adversity, cross-national research by Gangestad and Buss (1993) linking mate choice and parasite severity was published. It, like Low's, was inspired by Hamilton and Zuk's (1982) parasite theory of sexual selection. According to that theory, physical attractiveness is a certification of genetic resistance to parasites—good genes for parasite resistance. Hamilton and Zuk provided data showing that, across species of birds, male plumage brightness was correlated positively with the prevalence of blood parasites in the birds. This finding indicates that sexual selection resulting from both female

mate preference for bright-plumaged males and male–male competition favoring bright-plumage males was stronger in the evolutionary histories of species with high parasite prevalence than in species with low infectious-disease stress.

Gangestad and Buss (1993) tested the parasite theory of sexual selection as applied to human mate choice. Specifically, they tested for a positive correlation across countries between human parasite severity and the importance people place on physical attractiveness in mate choice. They used data from 29 of 37 countries studied by Buss (1989) and Low's parasite-severity scores (mentioned earlier) for those 29 countries. Each participant in Buss' huge study—there were many thousands of participants—completed a questionnaire and rated the importance of 18 attributes as criteria for choosing a mate, including the variable of interest here, "good looks." Certain variables across nations (e.g., average income, world region) were statistically controlled. Gangestad and Buss (1993) reported a robust, positive correlation between the value people attribute to good looks in a mate and parasite severity, and the correlation was found in each sex. Gangestad and Buss (1993) argued that the psychological machinery responsible for their results may be a combination of (1) species-wide facultative (conditional) adaptation enabling people to track local parasite stress and, based on that assessment, to adjust the priority given to good looks, and (2) adaptations that are genetically different across regions and set a region-specific value on good looks of a mate. Both (1) and (2) are processes of the ontogeny of values that we discussed in earlier chapters. For reasons discussed in Chap. 3, (1) is likely to be the most general and widespread enculturation process, and even when (2) is involved, so, too, is conditional adoption of values.

More recently, Gangestad et al. (2006) expanded the 1993 Gangestad and Buss study by statistically controlling for some additional potential confounding variables (e.g., gender inequality); the 1993 results were upheld. Hence, there is considerable evidence for humans showing that high parasite stress evokes an elevated valuation given to physical attractiveness in a mate; correspondingly, low parasite stress evokes a lower priority placed on physical attractiveness. According to the parasite-stress theory of values, the high value given to physical attractiveness in parasite-rich areas is part of the behavioral immune system. As parasite stress increases across regions, men and women place increased importance on obtaining a mate that is physically attractive, because physical attractiveness is a marker of high phenotypic and genetic quality pertaining, in part, to the ability to resist local infectious diseases.

6.3.2 Women's Mate-Choice Trade-Off

There is also considerable evidence that women engage in a trade-off in mate choice because physically attractive men—men of high phenotypic and genetic quality—invest less in their romantic partners and in offspring than do physically unattractive men (reviewed in Thornhill and Gangestad 2008). Lee and Zietsch (2011) have studied this trade-off by priming women with either a questionnaire that contained

parasite-relevant cues (the perceived-vulnerability-to-disease (PVD) scale) or a questionnaire containing cues of food and other basic resource limitations. Following the primes, women indicated the importance to them in mate choice of a mate with earning potential and willingness to invest versus a mate with masculinity, creativity, and other traits thought to correspond to male genetic quality. (See Thornhill and Gangestad 2008 for a review of the evidence for certain male traits as markers of genetic quality.) For a control prime, they used a questionnaire unrelated to the two trade-off variables. Women primed by the parasite-prevalence cues prioritized a mate of high genetic quality more than women primed by the control or the resource-scarcity condition; women primed by parasite-salient cues showed the least preference for a male with the ability and willingness to invest. The women primed by the resource-scarcity condition showed the reverse pattern, with a maximum priority for an investing mate. This research indicates that women's perception of contagion in their current environment immediately activates the aspect of their behavioral immune system that enhances their psychological preference for a mate of high genetic quality—a mate that ancestrally would sire offspring with above average resistance to infectious disease.

6.3.3 Other Attractiveness Research

Lisa DeBruine et al. (2012) have provided additional evidence that high parasite stress evokes in women an enhanced preference for masculine men. They used a website that presented to women from many different countries men's faces that varied in testosteronization/masculinity and hence in facial markers of male phenotypic and genetic quality. (See Thornhill and Gangestad 2008 for a review of the evidence for male testosteronization as a signal of phenotypic and genetic quality, and Rantala et al. (2012) and Pawlowski et al. (2014) that have shown links between testosteronization and immunocompetence in men.) DeBruine et al. (2012) found that women's preference for testosteronization of the male faces correlated significantly and positively with our measure *Combined Parasite Stress* across 30 countries. They reported, too, that the same pattern occurs across the 50 states of the USA, using our measure of *Parasite Stress USA*. (These two measures of parasite stress are explained in Chap. 5.) Debruine et al. (2012) also discuss two earlier studies, one across the 30 countries and one across the 50 USA states, that they and colleagues conducted using the same facial stimuli, but somewhat different measures of parasite stress. These studies gave results similar to those with our measures of parasite stress. Hence, in countries and USA states with high parasite stress, women value men's good looks in terms of masculinity of the face more than in regions of low parasite stress. In related research, Moore et al. (2013) studied cross-cultural differences in women's preferences of composite images of male faces constructed to represent different combinations of features associated with high versus low cortisol and testosterone in men. With respect to pathogen stress variation across countries, they found that women from countries with higher levels of

pathogen stress strongly preferred testosteronization in male faces, which is consistent with the findings of Debruine et al. (2012).

Complementary research by Jones et al. (2013a) investigated the role of a measure of disgust sensitivity in women's judgments of the attractiveness of masculine facial features of men. They reported that individual differences in disgust sensitivity positively predicted these attractiveness judgments. Their other studies reported in the same paper examined women's disgust sensitivity in relation to their preferences for men's masculine voices and nonfacial bodily features. The same results were found for men's voices and bodily features as found with faces. In a separate study, Jones et al. (2013b) found that men's judgments of the attractiveness of feminine facial features (facial estrogenization) in women's faces positively related to the men's disgust sensitivity.

Little et al. (2010) experimentally manipulated cues of contagion risk presented to research participants using pictures of high and no parasite salience. They then measured the participants' attractiveness ratings attributed to human faces that varied in bilateral symmetry and hormone markers. Symmetry of bodily features, like sex-specific hormone markers in the face (estrogen markers in women's faces and testosterone markers in men's), probably depicts phenotypic and genetic quality and hence resistance to infectious disease (Thornhill and Gangestad 2008). Little et al. (2010) found that people who were exposed to cues of high contagion risk, compared to those seeing no contagion risk, showed increased facial attractiveness preferences for opposite-sex individuals with greater facial sex-specific hormone markers and symmetry.

A study by Welling et al. (2007), like those of DeBruine et al. (2012), Jones et al. (2013a, b), and Little et al. (2010), provided evidence that facial attractiveness judgments are a component of the behavioral immune system. Welling et al. linked facial attractiveness judgments of research participants of both sexes to the participants' PVD scores. As we have discussed, PVD, an aspect of the behavioral immune system, is an individual-difference measure created from people's responses to questionnaire items about their concern with contagion. Men and women who perceived themselves to be more vulnerable to infectious disease attributed higher attractiveness to faces separately rated as healthy (by nonexperimental participants) than did individuals who perceived themselves to be relatively less vulnerable to infectious disease.

A recent investigation by Young et al. (2011) built on those of Little et al. (2010) and Welling et al. (2007) just described. Young and colleagues conducted two studies to test the hypothesis that variation in people's disease concerns is related positively to the variation in which they value symmetrical faces versus asymmetric faces. Both studies involved both sexes judging faces that varied in symmetry. In one study, they measured individual differences among research participants in PVD. In the second study, they primed participants with infectious-disease-relevant pictures as well as control pictures and then measured their facial symmetry preferences immediately thereafter. In both studies, increased sensitivity to infectious diseases was associated with heightened value placed on symmetric faces. Notably, their results did not generalize to symmetric versus asymmetric nonfacial images.

Hence, these studies indicate that people have a specific preference for faces that are symmetric when infectious disease becomes more salient.

de Barra et al. (2013) investigated in Bangladesh the ontogeny of facial attractiveness judgments in relation to infectious diseases experienced during childhood. They reported that childhood illness, particularly episodes of diarrhea, positively relate to individual men and women's facial attractiveness ratings of sexually dimorphic faces of the opposite sex. Thus, an ontogeny of high infectious-disease encounters evokes an elevated preference in women for masculine faces and an elevated preference in men for feminine/estrogenized faces.

An interesting line of research has developed that seeks to determine whether people who have greater behavioral immune system reactivity avoid unattractive, unfit mating partners because they represent a potentially large cost of association or whether they are drawn to physically attractive mating partners because they represent an especially beneficial association. At this point, evidence has been found for both conjectures. Park et al. (2012) reported that people high in pathogen disgust assigned lower attractiveness ratings for otherwise determined unattractive targets, while for attractive targets, pathogen disgust was uncorrelated with attractiveness ratings. Meanwhile, Cantú (2013) reported that when pathogen prevalence was made temporarily salient, women showed a strong preference for physically attractive men; for men, this result did not emerge. The contrasting findings are intriguing and certainly point to the need for more research in this area.

6.3.4 Overview: Mate-Choice Studies

The research studies discussed earlier conducted by Gangestad and colleagues, Lee and Zeitsch, Debruine and colleagues, Moore and colleagues, Jones and colleagues, Little and colleagues, Welling and colleagues, Young and colleagues, and de Barra et al. provide mutually reinforcing evidence. In high-parasite regions, both sexes value a mate's looks more than in low-parasite regions, and men's masculinity becomes increasingly important in women's attractiveness judgments as parasite stress increases across regions. The research on the ontogeny of facial-attractiveness mate preferences indicates that individual people who have more infectious diseases during childhood possess a psychological mate preference for enhanced hormonal effects in faces that relates to a genetic immunity which results in offspring with elevated immunocompetence. In high parasite regions, more people experience an ontogeny of high infectious-disease encounters than in low parasite-stress regions. Furthermore, masculinity preferences in women are predicted by their disgust sensitivity. Regional variation in ontogenetic experience with infectious disease and the associated evoked degree of disgust sensitivity apparently combine to account for the regional differences in the importance of physical attractiveness of a mate across countries and states of the USA. Thus, it seems that a childhood of high parasite stress evokes higher disgust and simultaneously evokes more value placed on physical attractiveness than a childhood of low parasite stress. In addition to the evoked

stable differences in valuation of looks, people respond immediately upon viewing contagion risk and specifically by increasing their attractiveness ratings of two categories of traits (symmetry and hormone markers) that relate to increased health and genetic quality of a mate. Also, upon perceiving a parasite threat, women respond immediately by prioritizing male physical attractiveness and other good-genes markers in a mate over male resourcefulness and investment. Nevertheless, it is not clear whether people with higher levels of contagion concerns are particularly drawn to attractive people or avoid unattractive people. Overall, then, as parasite stress increases, so does the value of obtaining a mate with phenotypic and genetic quality pertaining to dealing with parasite adversity. Finally, people with high PVD value health cues and symmetry in faces more than people with low PVD.

All these studies are supportive of the enculturation process we described earlier in our book. People contingently adopt attractiveness values based on their local utility in defense against parasite adversity. This begins during childhood and tracks individuals to a given level of attractiveness valuation, creating individual differences as well as regional differences. These individuals, however, retain conditionality in their sensitivity to cues of local parasite threat, allowing them to modify their attractiveness-preference values as current circumstances of parasite threat wax and wane. These studies, as well as many others we discuss throughout the book, reveal the exquisite functional organization of the behavioral immune system. We anticipate that future research on values other than attractiveness judgments that are also features of the behavioral immune system will be shown to possess the same degree of exquisite functional design. Evidence we have discussed already in this book certainly indicates this is the case across values of collectivism–individualism.

The research by Welling et al. and Young et al. discussed earlier on PVD suggests a relationship between attractiveness judgments and collectivism–individualism. Although physical attractiveness is a significant social asset everywhere (Thornhill and Gangestad 1993), it may be especially salient in collectivist cultures, which are characterized by high parasite stress.

We hypothesize that the importance of having a physically attractive mate is correlated positively with conservatism across cultures and people. This hypothesis is consistent with (a) the positive relationship between parasite stress and importance attributed to physical attractiveness and (b) the greater value placed on facial health of a mate and on facial symmetry by high scorers on PVD than by low scorers. PVD scores across individuals positively correlate with conservatism (and negatively with liberalism) (see Chap. 4). However, as of yet, the direct relationship between the salience-of-looks variables and collectivism has not been studied.

6.4 Marital Divorce

We mentioned in Chap. 4 the relationship between people's core values and marital durability. Gelfand et al. (2004) discussed evidence that has shown that, across countries, collectivism–individualism is related to variation in marital divorce rates.

Vandello and Cohen (1999) provided evidence of the same pattern across states of the USA: the ratio of marriages to divorces was an item they used to measure states' collectivism (Chap. 5). Collectivists' marriages are more durable than are those of individualists. On the one hand, this pattern seems contrary to expectations. Collectivist marriages are based more often on family honor, duty and preference, norm conformity, and in-group social preference, and less so on romantic love between a man and woman. As the basis of long-term pairings and marriage, romantic love is more characteristic of individualist cultures and thus one might infer that love-based marriages would be more durable. On the other hand, individualists are more self-sufficient and independent, which appears to override the effect of love on duration of individualists' marriages and generate the overall higher divorce rate among individualists than among collectivists. Individualists' greater risk-proneness (acceptance of uncertainty, Chap. 4) may affect also their higher divorce rate.

Another factor that might contribute to higher divorce rates in individualistic cultures than in collectivist cultures is the greater sexual liberation of women (from traditional sexual values of caution and continence) and their associated reduced sexual restrictiveness in individualistic societies. In women, the value of reduced sexual restrictiveness may give them an opportunity to experience sexual intimacy with multiple men, which could contribute to partner desertion and switching. Given this, increased sexual liberation of women, characteristic of individualistic cultures, is expected to increase the divorce rate. In contrast to women's sexual restrictiveness, men's sexual restrictiveness is uncorrelated, or only weakly correlated, with collectivism–individualism. Probably contributing also to the higher divorce rate in individualistic societies is the relaxation of legal grounds for divorce in such societies, which was initiated during the sexual revolution of the 1960s in the West (Chap. 10). The relationships between sexual restrictiveness and both collectivism–individualism and parasite adversity have received attention from researchers, as we describe next.

6.5 Female Sociosexual Orientation

The Sociosexual Orientation Inventory (SOI; Simpson and Gangestad 1991) is a self-report questionnaire commonly used to assess a behavioral disposition toward unrestricted sexuality (e.g., willingness to engage in sexual relations in the absence of a long-term commitment). Based on data collected from 14,059 adults worldwide, Schmitt (2005) reported sex-specific average SOI scores for nearly 50 countries. High SOI scores indicate a more unrestricted approach to sexual behavior.

Using these data, Schaller and Murray (2008) found that parasite prevalence predicted both male and female mean SOI scores—more parasites, greater restricted sexuality—although only the relation with female SOI scores remained statistically significant after controlling for additional variables. Thornhill et al. (2010) analyzed the cross-national SOI scores again, but with the three types of human disease richness discussed in Chap. 5: human-specific, multihost, and zoonotic. Thornhill

et al.'s analyses focused exclusively on average female SOI. Across 45 countries, female SOI was correlated negatively with indices of both human-specific parasite richness ($r=-0.38$, $p=0.01$) and multihost parasite richness ($r=-0.47$, $p<0.001$). This pattern means that as parasite adversity declines, women become increasingly sexually unrestricted. The relation with zoonotic parasite richness was negligible and nonsignificant ($r=-0.12$, $p=0.44$). Hence, as in the research on collectivism–individualism (described in Chap. 5), human infectious diseases that are transmissible from human to human impact people's values, in this case women's sexual values, to a far greater extent than zoonotic diseases.

Furthermore, research done on individuals has found that people who have greater behavioral immune system reactivity, either by measuring constructs such as PVD or by manipulating parasite salience, demonstrated greater sexual restrictiveness in attitude and behavior, most especially women (Duncan et al. 2009; Murray et al. 2013).

It also has been shown that, across many countries of the world, women's sexual unrestrictiveness correlates positively with (a) individualism, (b) gender equality in opportunity and participation in societal matters, and (c) democratization (Thornhill et al. 2009). Hence, women's sexual liberation from traditional values of sexual continence is a component of overall liberalization of values. In Chap. 10, we treat further the so-called sexual revolution and women's liberation that occurred in the West in the 1960s and 1970s.

6.6 Inbreeding

6.6.1 The Hypothesis and Hoben et al. (2010)

It may appear counterintuitive to anchor the parasite-stress theory of sociality on the proposition that parasite stress leads individuals to remain in the local community and avoid distant members of the same species. Indeed, one hypothesized benefit of sexual reproduction and outbreeding is the genetic diversification of a brood of offspring in order to combat parasite threats (Tooby 1982; Trivers 1985; Hamilton et al. 1990; Ridley 1993). Shields' (1982) and others' ideas (Kokko and Ots 2006), however, indicate that inbreeding may be adaptive under a range of circumstances that give rise to outbreeding depression. We hypothesized that the costs and benefits of inbreeding and outbreeding will vary regionally primarily in accordance with variation in parasite severity (Fincher and Thornhill 2008a; b). In areas of high parasite severity, inbreeding is costly because it reduces variation in the molecular milieu from which an individual can mount an immune response (Penn and Potts 1999), but beneficial through the maintenance of locally adaptive, genetically based immune responses as well as the avoidance of infectious diseases that are not harbored by the local group. Thus, although close inbreeding is maladaptive under high parasite severity levels, distant outbreeding is too. This is because host–parasite coevolutionary races build complex, locally adaptive host immune adaptations

including coadapted gene complexes that often work best against infectious disease if not disrupted by distant outbreeding. Both coadapted gene complexes and local adaptation render some degree of inbreeding adaptive under high parasite prevalence, as first hypothesized by William Shields (1982).

We discovered that Abraham Buunk, Ashley Hoben, and Mark Schaller were independently thinking along the same lines we were about how parasite stress may promote inbreeding. We began collaboration in 2006 with them to test the prediction that parasite stress would show a positive relationship with inbreeding across contemporary countries of the world. That work is reported in detail in Hoben et al. (2010). People have psychological adaptation that functions to avoid mating with very close relatives, such as parents, and full- and half-siblings (Lieberman et al. 2003; Lieberman et al. 2007). Our hypothesis pertains to relatives more distant than these categories and especially cousins. Here we give a brief sketch of the research in Hoben et al. (2010).

As we were conducting our research, some evidence for the parasite-stress hypothesis for inbreeding appeared in the literature. Denic and Nicholls (2007; also Denic et al. 2008a, b) reported a positive correlation between malaria endemism and the frequency of consanguineous marriages across many countries of the world. Denic and Nicholls' theoretical reasoning was similar to our own. Their evidence is specific to just one of the many human infectious diseases that, historically, has been of differential prevalence worldwide. Hence, we wanted to test the hypothesis more generally by looking at human infectious diseases widely.

Consanguineous marriage occurs between genetic relatives (Thornhill 1991). Despite the negative effects for offspring produced from this type of marriage (e.g., inbreeding depression), it continues to occur at high rates in various parts of the world and typically involves various categories of cousins, and, in some cases, uncle–niece unions (e.g., Rao and Inbaraj 1977). Consanguineous marriage is especially prevalent among Muslim and Hindu populations in Africa and Asia (Jaber et al. 1998). For example, in Jordan, 50 % of all marriages are between genetic relatives, and in Kuwait and Saudi Arabia 54 %, whereas in India consanguineous marriages vary from 5 to 61 % depending on socioeconomic status, religion, and caste (Jaber et al. 1996). These rates are in sharp contrast to the low rate in western countries such as the United States (Jaber et al. 1998).

Our colleagues and we wanted to see if regional variation in consanguineous marriages might be explained by variable parasite stress. From Bittles (1998) we obtained data from 381 surveys that include information for millions of marriages (see www.consang.net) and data on the proportion of consanguineous marriages in 72 different countries. We used the index *Historical Parasite Severity* described in Chap. 5. In addition to the two variables of primary conceptual interest, we also assessed additional variables in order to address possible alternative causal explanations for the hypothesized relationship between historical pathogen severity and consanguineous marriages.

In support of the parasite-stress hypothesis of inbreeding, we found that *Historical Parasite Severity* positively and significantly predicts regional differences in the percentage of consanguineous marriages: $r = 0.40$ ($p < 0.001$). As we

have mentioned earlier in our book, parasite severity is negatively correlated with economic wealth within a region—wealthy nations have less parasite adversity than poor nations (Fincher et al. 2008, Chap. 11). Therefore, the significant positive correlation between parasite severity and consanguineous marriages might be a spurious result of a negative relation between economic wealth and consanguineous marriage; however, we found no support for this alternative explanation. When *Historical Parasite Severity* and gross domestic product per capita (GDP per capita; 2009 data obtained from the *CIA World Factbook*; www.cia.gov) were entered jointly as predictors of consanguineous marriages, the effect of GDP per capita was weak and nonsignificant (std. $\beta = -0.17$, $p = 0.13$); the effect of pathogen severity was reduced slightly, but still remained stronger than that of GDP per capita (std. $\beta = 0.37$, $p = 0.001$).

Moreover, because it has been observed previously that consanguineous marriage is more common in regions in which malaria is endemic (Denic and Nicholls 2007), we felt it is important to see if the effect we found is driven primarily or only by malaria's prevalence. This was not the case. We conducted an analysis in which *Historical Parasite Severity* was entered along with the specific prevalence of malaria as predictors of consanguineous marriage. Results indicated no unique effect of malaria prevalence ($\beta = 0.02$, $p = 0.92$); but the overall index of historical pathogen severity remained a significant predictor of consanguineous marriage (std. $\beta = 0.35$, $p = 0.04$). Hoben et al. (2010) examined analytically a number of other alternative conjectures about the causes of cousin marriage and found that, when they are considered, the positive relationship between the prevalence of consanguineous marriage and parasite severity remains statistically robust.

We also computed the historical severity of parasites and the percentage of consanguineous marriages within each of the six cultural areas of the world identified by Murdock (1949), and conducted additional analyses in which we treated these six world regions as the units of analysis. Although the sample size of six is very small, it is noteworthy that the correlation between pathogen severity and consanguineous marriage replicates the positive correlation observed in our cross-national analysis ($r = 0.56$). Thus, in cultural regions with a higher historical severity of parasites, there is a higher frequency of consanguineous marriage, and there are probably no exceptional regions in this overall pattern.

In sum, historical pathogen prevalence was a substantial and significant predictor of regional differences in consanguineous marriages, and this effect does not appear to be a spurious result of other variables associated with pathogen prevalence. These results are consistent with the hypothesis that regional differences in consanguineous marriage emerged, in part, because consanguineous marriages conferred immunological resistance to local pathogens and that these adaptive benefits accrued primarily in geographical regions with high levels of parasite severity.

In our study with colleagues on inbreeding, we felt it was of interest to consider the effect of historical pathogen severity on consanguineous marriage alongside other cross-cultural differences that are predicted by parasite adversity. In regions with high levels of pathogens, people (especially women) have more restricted approaches to mating, as discussed in Sect. 6.5 on female sociosexual orientation. People in such regions also are more likely to endorse collectivist values that

emphasize within-group interdependence, extended-family nepotism, neophobia, xenophobia, and philopatry, as documented in Chap. 5. All of these characteristics are conceptually consistent with increased inbreeding. As expected from this consistency, additional analyses in Hoben et al. (2010) revealed that correlations between consanguineous marriage and cultural values result, in part, from shared variance with parasite severity. For example, the two measures of collectivism examined (*Gelfand In-group Collectivism* and *Kashima Collectivism*; see Chap. 5) were correlated positively with consanguineous marriage (r's = 0.31 and 0.29), but, when controlling for historical pathogen severity, these correlations were reduced (partial r's = 0.22 and 0.09). Thus, while the broader cultural value system in a region may reinforce behavioral norms promoting or inhibiting inbreeding (and, in turn, be reinforced by inbreeding norms), evidence indicates that the cultural values of collectivism–individualism are tied to patterns of inbreeding–outbreeding by way of underlying parasite stress.

6.6.2 Hoben's Dissertation

Ashley Hoben wrote her doctoral dissertation on human inbreeding and outbreeding while she was a student at the University of Groningen in the Netherlands (Hoben 2011). The published paper Hoben et al. (2010) (discussed earlier) was one chapter of her dissertation. Here we describe her other doctoral studies contained in her dissertation. First, using parasite-severity data from Low's research (discussed in Sect. 6.2.1), she discovered that the cross-national pattern of inbreeding marital frequency showing a positive relationship with parasite stress is repeated in the sample of indigenous human societies comprising the Standard Cross-Cultural Sample. Hoben used "first-cousin-marriage allowed" versus "not allowed" as her inbreeding variable. Her analysis controlled for variables that she felt were potential confounders. The end result was that parasite stress significantly and positively predicts the value of permitting versus the value of not permitting first-cousin marriage across the indigenous societies in the ethnographic record of anthropology. Said differently, in ethnographic societies facing low parasite stress, there is greater outbreeding than in societies facing high parasite stress.

The question of why consanguineous marriage occurs in some indigenous societies and not others has been a long-standing one in anthropology. (See a review of this research history in Thornhill and Thornhill 1987.) Hoben's research places this question in a bigger intellectual framework and provides a more encompassing and convincing answer. Evidence indicates that the answer is the same for inbreeding variation across indigenous societies as for the variation in inbreeding across contemporary countries. Even more synthetic is that both patterns of inbreeding predicted by parasite stress are now patterns that provide partial support for an overarching theory of sociality—the parasite-stress theory of values.

Hoben made some additional relevant discoveries that are reported in her dissertation. She obtained the opinions of the Dutch students at her university about various scenarios describing romantic relationships or marriage among cousins.

Based on the relatively low parasite stress in the region of her study, she predicted from the parasite-stress theory of values that there would be a general negativism toward such relationships—that is, a general preference for outbreeding. The prediction was supported significantly across a range of experimental designs. The liberal-minded students who attend university in the Netherlands are open-minded in general, as is typical of liberals, but that openness stops when it comes to inbreeding. Their preference was for outbreeding, with inbreeding viewed negatively or even as immoral sexuality.

6.7 Male Sexual Competition

6.7.1 Out-Group Men as Sexual Competitors

It is well established that conservatism and its associated high PVD are related to many types of prejudice, including prejudices against foreigners and immigrants (Chaps. 3–5). Klavina et al. (2011) expanded knowledge of this pattern by investigating the relationship between out-group prejudice and competition for mates in the Netherlands. In one study of their investigation, they presented Dutch research participants of Dutch ancestry with a bogus newspaper article that described Italians (out-group immigrants) as a mating threat by being attractive, in high numbers, and marrying Dutch-in-group members. Men read an article that depicted out-group men as sexual competitors; women read an article that depicted out-group women as sexual competitors. A control group of participants of each sex read a bogus article that described the absence of interest among in-group people in dating and marrying Italians. They also measured the research participants' PVD and their out-group prejudice using standard and validated questionnaires. They hypothesized that the mating-threat prime would increase the male research participants prejudice toward out-group men and especially so in high-PVD male research participants. Their data supported this hypothesis. They found, however, no statistically significant patterns for the women research participants.

Klavina et al. (2011) proposed that males only are expected to show the pattern because they have been under stronger sexual selection for high mate number than women have, and hence value mate number more than women do. The main out-group threat for women is violent out-group men, not out-group women. Out-group men pose the potential threats to women of kidnap and sexual coercion (Thornhill and Palmer 2000; Navarrete et al. 2009, 2010). Sexual coercion circumvents female mate choice and thus reduces female reproductive success. McDonald et al. (2011) reported that women's bias against out-group men, who they perceive as physically formidable, increases during estrus (the several fertile days of an ovulatory menstrual cycle, Thornhill and Gangestad 2008). Estrus is associated with maximum cost to women of sexual coercion, because it is the time of conception and hence of sire determination of an offspring. PVD was predicted by Klavina et al. (2011) to

influence men's prejudice toward out-group mating threat because prior research has shown PVD's positive relationship with prejudice (Chap. 4).

Klavina et al. (2011) conducted a second study in their investigation. In this experiment, they gave Dutch men a series of infectious-disease salient pictures known to increase PVD. They showed other Dutch men control pictures that depicted either neutral situations or dangerous situations unrelated to contagion threat. Then, all of these participants read the bogus article that described Italian men as a mating threat. After that, prejudice toward out-group men was measured. This experiment repeated the results in the first study discussed earlier. Men primed with infectious-disease cues in pictures, but not men not so primed, increased prejudice toward out-group men. The results of the two studies revealed that it is the Dutch men's assessment that Italian men are competing successfully for Dutch men's potential mates, in combination with heightened perceived vulnerability to contagion, that result in increased negative attitudes toward Italian (out-group) men.

Klavina et al. (2011) mention that their results imply that the perception of mate-competition threat from out-group and associated out-group prejudice is stronger in collectivist men than in individualist men. The separate finding that conservatism and PVD are robustly and positively correlated (see Chap. 4) supports this link and thus their suggestion. They mention, too, the implication of their finding for inter-group coalitional aggression, which is almost exclusively perpetrated by men. Collectivist men's negativism about out-group men poaching in-group women may be an important factor causing the documented positive association between collectivism and frequency of civil conflicts across nations (see Chap. 12 on warfare, parasite stress, and values).

6.7.2 White-on-Black Violence

Klavina et al.'s (2011) findings allow a deeper understanding of some collectivist men's prejudicial custom of segregating and perpetrating violence on out-group men. A well-studied example is the USA, primarily in the South, from the period of Reconstruction (following the American Civil War) and into the 1960s. Historians have documented the racist practices of white supremacist mobs of men castrating, mutilating, shooting, burning, and lynching African-Americans and destroying their property and communities over this period (e.g., Brundage 1993). The documentation shows that most of the violence was directed at black men, less commonly black boys (pre-reproductive-age males), and the least at females. Violence was perpetrated on females when they tried to defend the men who were the focus of white supremacist prejudice and violence. Violence was perpetrated on black men as a result of alleged homicide, rape, attempted rape, or the disrespect of whites or other violations of Old South customs of racial segregation.

Historians have documented that this violence contributed importantly to the great mass migrations of blacks from the South that began after the USA Civil War and continued into the 1960s (Wilkerson 2010). A combination of economic dire

straits for southern blacks and threatened physical pain or death at the hands of racist mobs is a strong incentive to immigrate, even for these highly philopatric people. Both of these emigration factors were generated by the highly conservative values held by southern whites that dehumanized and disenfranchised black people. Collectivism's value of inequality not only restricts resources, opportunity, and participation in society to those of the privileged group (by birth, color, or class), but also can lead the privileged group to more directly exterminate out-groups.

The have-and-have-not classist culture of the Old South also impacted negatively a large portion of the white population. The plight of the average white southerner during this period was dire, given the overall undemocratic societal system and extreme wealth inequality generated by the conservative political regimes of this era. Key (1949) has documented that two central and persistent issues anchored the politics and policies of the governing bodies of the Old South: economic and political disenfranchisement of blacks and poor whites.

Historians typically explain the white-on-black violence of the era in terms of white racism. This is certainly correct, but the Klavina et al. (2011) study discussed earlier adds new depth to this explanation. We suggest, the southern men who perpetrated the violence not only hated blacks, they also feared them, because they perceived them as both a contagion risk and a mating threat. The unbridled sexual motivation of black men to sexually access white women was a widespread ideological deduction among whites in the conservative culture of the Old South. Then and there it was normatively taboo for a black man to be alone with or touch a white woman. Also, romantic or sexual interactions between white women and black men were illegal. White men in the Old South were often quick to condemn black men for perceived sexually inappropriate behavior toward white women (Hodes 1999).

We have investigated a prediction from our thinking here: lynchings across USA states of blacks will be correlated positively with parasite adversity and collectivism. Data exist to allow an initial test. Data on lynching of blacks by whites, collected from newspaper articles, are archived at Tuskegee University (Tuskegee Archive: http://law2.umkc.edu/faculty/projects/ftrials/shipp/lychingstate.html). The data extend over the period 1882–1968, by state. As predicted, both relationships were found, and are statistically significant. Lynchings of blacks by whites are correlated with *Parasite Stress USA* very strongly: $r=0.71$, $p<0.0001$, $n=44$ states for which data are available. Collectivism (based on Vandello and Cohen 1999) shows a moderate relationship with the lynchings: $r=0.46$, $p=0.0021$, $n=44$. Note that the lynching data are not rates based on population estimates as are the rates of other types of homicides we analyze in Chap. 8. Rates would be impossible to compute because of the changing social structure over the period covered by the lynching data. Although lynchings and other white-on-black violence has been much discussed by historians of the South, to our knowledge this is the first analysis that ties the regional variation in the violence to an evolutionary theory of human sociality.

Racism-inspired lynchings are right up there with Nazi and other holocausts in anchoring the most horrific pole of the dimension of "man's inhumanity to man," as the poet Robert Burns famously labeled hurtful prejudice in general. According to

the parasite-stress theory of values, much of the variation across the entire dimension of intolerance and hate is caused proximately by variable parasite stress and associated evoked values. According to the same theory, it is caused ultimately by past Darwinian selection in the context of variable parasite adversity that crafted condition-dependent values-adopter psychological adaptation.

6.8 Disgust and Sexual Arousal

In earlier chapters, we discussed the emotion of disgust as an adaptation that defends against contagion. A range of stimuli cues disgust: diseased people, vermin that imply contagion risk, and even certain norm or moral violations. Evolution-minded researchers interested in the functional design of disgust have proposed that disgust should be organized functionally to show little or no activation under conditions that have infectious-disease risk, but if these conditions are not tended to or pursued (rather than avoided) would reduce inclusive reproductive success (Oaten et al. 2009; Curtis et al. 2011). Imminent sexual opportunity is a context in which disgust sensitivity to sexual risks of contagion should show design for reduction in order to promote sexual intercourse and hence male mating success.

6.8.1 Women's Sexual Arousal

Borg and de Jong (2012) investigated women's disgust sensitivity in relation to their sexual arousal. Female participants were placed into one of three groups: sexual arousal, nonsex positive arousal, or a control group. After watching video clips meant to stimulate the proper mood, participants were faced with participating in sex-related disgust activities or nonsex disgust activities in order to measure their avoidance behavior. Women who were sexually aroused participated in more disgusting activities (both sex-related and nonsex), suggesting a reduction in disgust sensitivity due to sexual arousal. Fleischman (2014) reported on an ongoing study of women's sexual arousal and disgust that also used films to elicit different mood states. Rather than measure sexual arousal subjectively as in Borg and de Jong (2012), they used a vaginal photoplethysmograph to detect sexual arousal. Additionally, to control for menstrual cycle variation, they tested all participants at about the same point in their respective menstrual cycles. Fleischman and colleagues found that women who were more disgust sensitive prior to the manipulation actually became more disgusted after sexual arousal, and women who were less disgust sensitive became less disgusted after becoming sexually aroused. Fleischman suggests this may mean that women who have well-functioning immune systems (those with low baseline disgust sensitivity) and can afford exposure to disease cues reduce the disgust sensitivity during sexual arousal, while those women with less effective immune systems—those that cannot afford exposure to disease cues—will actually increase disgust sensitivity during sexual arousal.

6.8.2 *Men's Sexual Arousal*

Stevenson et al. (2011) examined the conditional expression of disgust in men under sexual arousal. They assigned men to one of four groups that viewed pictures: one group viewed erotic women's pictures, a second group viewed nonerotic images of women, a third group viewed pleasant, but nonerotic-arousing images, and the fourth group viewed unpleasant, but arousing images (e.g., a gun aimed at them). Then, all the men viewed paired images of actual disgust elicitors; each pair contained a sexual disgust image and a nonsexual disgust image. The paired stimuli (sexual and nonsexual) were repeated with validated tactile and auditory disgust elicitors. Finally, the men's disgust level was measured with the Disgust Sensitivity Scale, a widely used, validated metric measuring disgust intensity. Men in the erotic-image group reported more sexual arousal than men in the other three groups; they also showed less disgust from sex-related disgust elicitors across the three types of sexual disgust elicitors than men in the other groups, and the lowering of disgust sensitivity in the erotic-image group was specific to sex-related disgust elicitors, not disgust in general. Hence, sexually aroused men adjust by lowering their disgust sensitivity, whether cued visually, tactilely, or auditorily, specifically to the sex-related component of disgust. Also, types of arousal other than sexual used in the experiment did not affect men's sexual disgust sensitivities. General arousal or even fear did not change men's sensitivity to sexual disgust elicitors.

Stevenson et al.'s (2011) findings provide evidence that men's sexual motivation is designed to interface with a part of the behavioral immune system—disgust sensitivity—in the way predicted by the parasite-stress theory of sociality. These findings imply something quite remarkable about disgust's functional design when it is remembered that people are functionally designed to accept many false positives in terms of stimuli suggestive of contagion risk (Chap. 3). Although this acceptance is well established, disgust's design shows nuances that prevent its typical activation from interfering with men's mating success, even though mating carries contagion risk. Though undeveloped, Fleischman (2014) offered the intriguing hypothesis that sexually transmitted diseases could benefit by somehow reducing disgust in order to increase their transmission rate. She was agnostic on this point, but such diseases would likely get the best payoff by focusing on male sexuality.

6.9 Sex Differences in Sickness Behavior and Suppression of Sexual Activity

Sickness behavior refers to the suite of behaviors that ensue once an individual becomes sick. This can include weakness, malaise, depression, lethargy, and the like (reviewed in Avitsur and Yirmiya 1999). One intriguing research finding (Avitsur and Yirmiya 1999) is that, under experimental exposure to infectious disease cues such as injections of lipopolysaccharide (an important constituent of

the outer membrane of Gram-negative bacteria), female rats show sickness behavior and a suppression of sexual activity. Male rats, on the other hand, do not suppress sexual activity, though they show other symptoms of sickness such as fever and reduced food consumption. Avitsur and Yirmiya (1999) suggested that the female suppression of sexual activity when sick may be a protective mechanism for avoiding conception while infected. They said that males "… seem to conceal their sickness when presented with an estrous female" (p. 793), and argued this was a strategy that functions in increasing male mating opportunities. Currently, it is unknown how carrying a current infection affects the sexual psychology of humans, but it is possible to investigate. A researcher could "infect" participants with endotoxins (e.g., lipopolysaccharide, Olsson et al. 2014; Schedlowski et al. 2014) and measure subsequent changes in their sexual attitudes or mate preferences.

6.10 Summary

The parasite theory of sexual selection, first discussed in detail and tested by Hamilton and Zuk in 1982, inspired research on the variation in marital systems across human indigenous societies. The variation in marital systems studied was the presence of monogamy versus polygyny and the degree of polygyny. Low (1988, 1990, 1994) and Marlowe (2003) reported that, across the traditional societies archived by anthropologists in the Standard Cross-Cultural Sample, parasite-stress scores are correlated positively with the degree of polygyny observed and recorded by anthropologists. Hence, as parasite stress increases across these societies, an increasingly small percentage of men monopolize more of the direct reproductive success of women. According to the parasite theory of sexual selection, this pattern is expected because high parasite stress generates high variation in the phenotypic and genetic quality of men, which then makes polygynous marriage adaptive for women, even though they must share a husband's resources with harem wives.

We hypothesize that collectivism is the value system that mediates the relationship between polygyny and parasite stress in the ethnographic record of anthropology. This is consistent with ethnographic accounts of Western polygyny and with certain research findings in social psychology.

Gangestad and Buss (1993) and Gangestad et al. (2006) conducted cross-national research inspired by the parasite theory of sexual selection that empirically linked human mate choice and parasite stress. They reported a positive correlation across countries between human parasite stress and the importance people place on physical attractiveness in mate choice. This finding was made from their reasoning that physical attractiveness is a certification of genetic resistance to parasites—good genes for parasite resistance—and hence is expected to be valued more in high than low parasite-stress regions.

The parasite theory of sexual selection is a subcategory of the more general and encompassing parasite-stress theory of values. The research studies reviewed in the chapter show that, as parasite stress increases, so does the value of obtaining a mate with phenotypic and genetic quality pertaining to dealing with parasite adversity.

Collectivists' marriages are more durable than are marriages of individualists. We argue that this difference is caused by the distinct values of conservatives versus liberals related to family ties, women's sexual restrictiveness, and adherence to traditional sex roles.

Parasite stress predicts positively women's sexual restrictiveness (continence) across many countries of the world. Specifically, as parasite stress declines, women show increased importance placed on having sexual relationships without commitment (less sexual restrictiveness). Nonzoonotic human parasites affect this pattern much more strongly than do zoonotic human parasites. Cross-national evidence indicates that women's sexual liberation from traditional values of sexual continence is a component of overall liberalization of values.

The frequency of consanguineous marriage varies greatly across contemporary countries and indigenous societies in the ethnographic record. We have hypothesized that a benefit of consanguineous marriage is keeping coadapted alleles together that defend against local parasites. Hence, as parasite stress increases across cultures, the parasite-stress theory of values predicts that people will engage in increased marital inbreeding and reduced marital outbreeding. Research findings support this hypothesis both cross-nationally and across indigenous cultures.

Klavina et al. (2011) showed that aspects of men's prejudice against out-group, immigrant men derive from the perception that the out-group men will mate with in-group women. They found, too, that this prejudice is related positively to men's PVD, which implies conservative men show more of the prejudice than liberal men. The violence and terrorism perpetrated by white men on African-American men in the Old South are informed importantly by Klavina et al.'s study. Stevenson et al. (2011) showed that men's sensitivity to sexual disgust is condition dependent. Sexually aroused men show reduced sexual disgust, but not reduced disgust in other disgust domains. Also, that effect was specific to sexual arousal, not general arousal. Their research implies sophisticated functional design of men's sexual disgust. Like other kinds of disgust, it functions to protect against contagion risk, but is moderated when men's mating opportunities arise.

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