environment, echoing the Marxian dictum "*Das Sein bestimmt das Bewußtsein*". To be convinced that an important part of our history is phylogeny and that our ancestors have been shaped by mutations and the forces of selection and to defend that position demands a strong person. In two books, Hiram Caton criticized radical feminism and other political movements for trying to undermine the family as the basic unit of society and its crucial role for successful early ontogeny.

Hiram was courageous in the choice of his research topics and in making his findings public. In contrast to many members of the older (my) generation, he really came to grips with computer technology and all the new options it facilitates. Hiram served as ISHE Information Officer from 2005 to 2008, and we on the board of ISHE benefitted from his drive and knowledge. He urged us to have a better relationship with the scientific press and the academic world. Yet, we still don't have a "press room" where new findings from ISHE colleagues would be presented, in a professional way, to those who mediate them to the interested public. Other scientific societies and especially big scientific institutions (e.g. the *Senckenberg Gesellschaft für Naturforschung* in Germany) have gone this way by now. We in the board of ISHE will have to see how we will position ourselves, a relatively small international society, in the shark tank out there.

I thank Hiram for his role in a crucial time of ISHE and we will miss his company, his Australian humor, his provocative ideas, and the talks around a fireplace.

Wulf Schiefenhövel, Ph.D., co-founded ethnomedicine in Germany, performing field studies in New Guinea on traditional medical beliefs and practices. Since then, he has done continuous fieldwork in ethnomedicine, anthropology, and human ethology, mainly in Melanesia and Indonesia, authoring 300 papers, either authoring, coauthoring, or coediting 24 books, and publishing scientific films.

Theoretical Articles

Understanding Sex Differences in Human Mortality Rates through Tinbergen's Four Questions

By **Daniel J. Kruger**
School of Public Health, University of Michigan, Ann Arbor, MI 48109

And **Carey J. Fitzgerald**
Department of Psychology, Central Michigan University, Mount Pleasant, MI 48859

Abstract

Sex differences in human mortality rates emerge from a complex interaction of genetic heritage and developmental environment. Although mortality is not in itself a behavior, it is an indirect product of behavior and physiology and thus responsive to life history variation in resource allocation, behavioral tendencies, and relevant environmental conditions. The explanatory framework of Tinbergen's Four Questions is sufficiently powerful in generalization to promote understanding of this phenomenon. Excess male mortality is a result of a trade-off between competitiveness and longevity. Male life history gives greater emphasis to reproductive effort at the expense of somatic effort, and mating effort at the expense of longevity compared to female life history. Men exhibit riskier behavioral patterns and greater physiological susceptibility, dying at higher rates from behavioral and most non-behavioral causes across the lifespan. The magnitude of the sex difference in mortality in developed nations peaks when males sexually mature and enter

into mating competition. Social and environmental conditions intensifying male competition for resources, status, and mates lead to increased male mortality.

Keywords: Tinbergen, Four Questions, Sex Differences, Sexual Selection, Mortality

Introduction

Being male is now the single most prominent demographic risk factor for early mortality in highly developed societies (Kruger & Nesse, 2006). Numerous studies document sex differences in longevity and mortality rates, yet those researchers lacking an evolutionary framework are still grasping for a full understanding despite statistically powerful data driven models (e.g., Rogers, Hummer, & Nam 2000). Darwin (1871) considered male intrasexual competition the best explanation for why mammalian males are significantly more physically aggressive than females. Long after Darwin's insights, most explanations of sex differences in human aggression, violence, and mortality are still based only on proximate factors. In the past few decades there has a been a revival of the recognition that such sex differentials emerge from an interaction of characteristics shaped by sexual selection and environmental conditions of development (e.g., Daly & Wilson 1978).

Although mortality is not in itself a behavior, it is an indirect product of behavior and physiology and thus responsive to life history variation in resource allocation, behavioral tendencies, and relevant environmental conditions. Tinbergen's (1963) Four Questions framework is sufficiently powerful in generalization to promote an integrated understanding of this phenomenon. Each of the Four Questions represents a unique and necessary aspect for a comprehensive explanation. Such a framework helps illustrate the complex network of relationships between causes emerging at different levels, maintaining an appropriate balance between the reductionism necessary to isolate independent mechanisms and the holistic understanding of the interrelationships among causes and mechanisms. Tinbergen includes the evolutionary (ultimate and integrative) causal explanations of adaptation (function) and phylogeny (evolutionary history), as well as the necessarily mechanistic explanations of more immediate (proximate) causal mechanisms and their ontogeny (developmental processes) during the lifespan of the individual.

Before discussing sex differences in mortality rates, it may be informative to outline evolutionary theory regarding mortality in general. One may initially wonder why evolutionary processes occurring over billions of years and millions of generations have not led to perfected complex organisms that can live indefinitely. However, the processes of natural and sexual selection maximize the survival of genes rather than the survival of individuals or species (Williams, 1957; Dawkins, 1976). Building and maintaining a body is in the service of reproduction: our bodies are essentially vehicles for the propagation of genetic information. The effort an individual expends on building and maintaining a body is ultimately for the purpose of reproduction.

Many genes have multiple effects (this is referred to as pleiotropy), which can be both beneficial and hazardous based on the developmental and environmental context. Genes with early benefits but later costs will be selected for because younger individuals have a higher reproductive value (Medawar, 1952). Selection pressure was greater at younger ages because few people survived to old age in ancestral environments, thus early acting beneficial genes spread faster than late acting beneficial genes. The cumulative result of these factors is senescence, a decline of physiological function over time (Williams, 1957). The relatively higher importance of reproduction at the expense of survival for the sake of longevity

also forms the basis for sex differences in mortality rates ultimately created by the processes of sexual selection.

Evolutionary Adaptation

Each of Tinbergen's Four Questions represents a different, independent but interconnected aspect of a more comprehensive explanation. In this case, it may be most useful to begin the discussion with the evolutionary history underlying sex differences in mortality. The ultimate functional framework provides a deep understanding of the systematic origins of excess male mortality, of course not considering mortality as an adaptation per se. Stable aggregate sex differences result from sexual selection, the processes of intra-sexual competition and inter-sexual selection, as well as selective pressures related to sex specific roles such as gestation. The basic properties of sexual reproduction define the male and female sexes, and explain why they differ from each other.

The vast majority of complex animal life reproduces sexually across generations. Genetic recombination helps purge harmful mutations, and genotypic variability facilitates adaptation to changing environmental conditions (Williams, 1975); competition from other species (Bell, 1982); predators and parasites (Williams, 1975); countering the adaptations of prey to predation; and starvation (Bell, 1982). Sexual reproduction entails the combination of gametes from a pair of parents. Larger gametes give zygotes greater viability; production of smaller gametes gives quantitative advantage and smaller gametes will be relatively more successful than intermediate sized gametes when large partner gametes are present. Thus, there is disruptive selection for gamete size (Bulmer & Parker, 2002). The definition of sex follows from this divergence in gamete size; females contribute larger gametes than males (See Figure 1). The cascade of effects responsible for aggregate differences between females and males originates from this sex difference in investment.

Figure 1. *Divergent Selection Pressure Leads To the Fundamental Sex Difference in Parental Investment.*
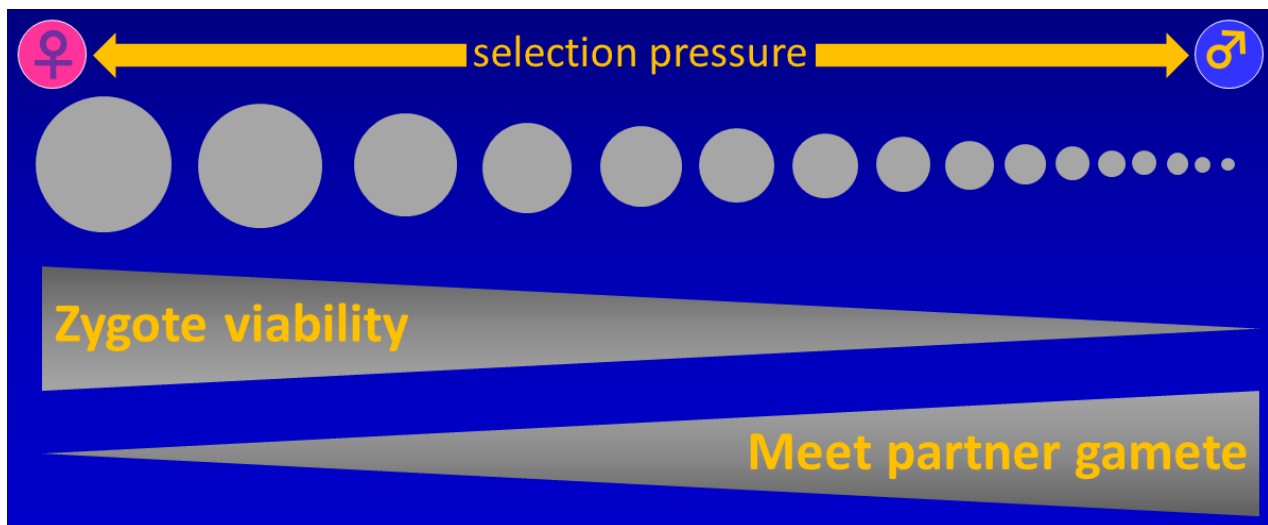
Because females usually invest considerably more than males in offspring, and are more limited in the quantity of offspring they can produce, they are selected to be choosier in considering partners (Bateman, 1948; Trivers, 1972). Male reproductive success is largely dependent on securing mating opportunities, through both intrasexual competition with other males and by being chosen by females in intersexual selection because of the

attractiveness of their traits and displays (Darwin, 1871). Male reproductive success is driven by sexual access to fecund females and genes enhancing sexual access and offspring production will be selected for even if they also increase risk of injury, sickness, and early death (Daly & Wilson 1978; Möller, Christe, & Lux 1999). For example, male guppies devote less time to foraging when novel females are present and those able to mate with a series of unfamiliar females will exhibit lower lifetime growth, demonstrating the trade-off between somatic and reproductive effort (Jordan & Brooks, 2010).

Mammalian male reproductive success usually benefits more than female reproductive success from a greater number of sexual partners and the greater variation in male reproductive success compared to females heightens male competition for reproductive access to females (Bateman, 1948; Trivers, 1972). This selected for relatively higher male investment in reproductive effort at the expense of somatic maintenance and relatively higher investment in mating effort at the expense of parental effort (See Figure 2, males allocate more effort to aspects highlighted in gold, at the expense of effort for alternative aspects within sets). Compared to women, men on average have greater height and weight, more upper-body strength, higher metabolic rates, and later sexual maturity (for a review, see Miller, 1998). These attributes facilitate direct male competition for mates, as well as competition for the resources and social status that make men attractive to prospective partners (Wilson & Daly, 1985).

Figure 2. *Male Investment Bias in Life History Strategy.*
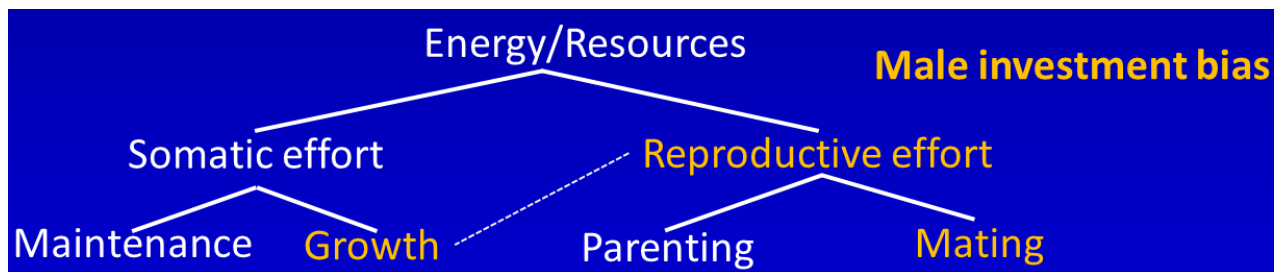
Male tendencies for risky behavior were selected for because they ultimately enhanced reproductive success, through the promotion of social status, resource control, and success in mating competition (Wilson & Daly 1992). Historically, men who controlled more resources married younger women, married more women, and produced offspring earlier (Low, 1998). Women across cultures value male social status and economic power (Buss, 1989) and these predict male reproductive success across a wide variety of societies (see Hopcroft, 2006). There is some differentiation of status even in relatively egalitarian foraging societies, and higher status men have better mating success (Chagnon 1992; Hill & Hurtado 1996).

Male competition can be hazardous, violent, and sometimes fatal (Betzig, 1986; Kaplan & Hill, 1985). Because sex differences in parental investment and mating competition are ultimately responsible for sex differences in mortality rates, we predict that the intensity of male mating competition (in interactions both within and between groups) will be proportional to the degree of excess male mortality.

Campbell (1999) concurs that aggression and violence have a much greater role in reproductive strategies for men than for women and agrees that sex differences in parental investment are the ultimate explanation. However, she emphasizes the greater potential

harm for women's reproductive success as the primary factor, as child survival is threatened more by maternal than paternal death. Taylor, Klein, Lewis, Gruenewald, Gurung, and Updegraff (2000) also build on sex differences in parental investment to argue that in contrast to the male biased fight or flight response, women respond to threats by tending and befriending in order to cultivate strong social bonds and protect the vulnerable.

Phylogeny

Cross-species comparisons provide valuable insights on the relationship between reproductive strategies and the relative sex difference in mortality rates. Tracing phylogenetic patterns helps reconstruct the evolutionary origins and history of attributes and behaviors, identifying both promoting and constraining influences on excess male mortality. Females typically outlive males across most animal species (Hazzard, 1990), reflecting trade-offs that increase male reproductive success even at the expense of longevity (Møller, Christe, & Lux 1999).

Reproductive patterns influence the intensity of sexual selection for each sex. Sex differences in physiology and behavior follow from the degree of polygyny, which could be thought of as the extent of male reproductive inequality. Polygyny is common amongst mammalian species, likely due to the relative male specialization in mating effort and female specialization in infant care and nutritional provisioning (Low, 2003, 2007; Reichard & Boesch, 2003). In highly polygynous species, a few males virtually monopolize reproductive success, creating powerful selection for traits that lead to success in mating competition, even if these traits are also detrimental to the health and longevity of high proportions of individuals (Williams, 1957; Kirkwood & Rose, 1991; Stearns, 1992). Species with higher degrees of polygyny have greater male competition and relatively more risky male behavior (Plavcan, 2000; Plavcan & van Schaik 1997; Plavcan, van Schaik, & Kappeler 1995), larger size and armor of males, and higher male mortality rates as compared to females (Leuttenegger & Kelley 1977). After controlling for the effects of phylogeny, there is a strong association between sexual size dimorphism and sex differences in mortality across mammalian taxa, demonstrating the role of the intensity of sexual selection (Promislow, 1992).

Across vertebrate species, the longevity gap between males and females is predominantly for polygynous species (Clutton-Brock & Isvaran, 2007). Elephant seals often illustrate the properties of polygyny in educational texts and presentations. Male elephant seals compete for control of harems of about 30 females and male reproductive success is highly skewed. Males who control harems obtain the vast majority of matings and 80% of males die before reproducing. Male development takes twice as long and adult males are three to four times the size of females (Harvey & Clutton-Brock, 1985). Similar patterns occur in other highly polygynous species such as peacocks and peahens.

Male primates compete to gain access to desirable mates, making displays of status, warding off potential competitors with loud warning calls, demonstrating strength, fighting with other males, and in some species (humans and callitrichids) provisioning resources (Buss, 2005). Male langur monkeys engage in vicious competitions for control of harems, leading to high levels of male mortality (Hrdy, 1977). When two or more Barbary macaque males are near an estrous female, they engage in scream fights and true fights (Kuester & Paul, 1992). In scream fights, males approach each other within 10 meters and begin screaming at each other. These scream fights may escalate into true fights, including hitting, thrashing, and biting (Kuester & Paul, 1992). The rate of male physical injuries caused by other males increases sharply during mating season,

demonstrating the association with maximizing mating opportunities (Kuester & Paul, 1992).

Male Japanese macaques establish a social dominance ranking system based on physical aggression. Dominant males are more likely to mate with females during their fertile periods, though males favored in female mate choice sired more offspring regardless of their social dominance (Soltis et al., 1997).

Mitsunaga, Shimizu, Nozaki, Yanagihara, Domingo-Roura, & Takenaka, 1997). In savannah baboons, there is a very large positive correlation between male dominance rank achieved through successful fights with rival males and mating success (Alberts, Watts, & Altmann, 2003). Male yellow and anubis baboons form coalitions to fight a common male threat; male mating opportunities do not strictly follow to their rank in the dominance hierarchy (Bulger, 1993). Chacma baboons do not form coalitions, and male mating opportunities follow directly from social rank (Bulger, 1993).

Male orangutans lead a largely solitary lifestyle, using loud "long calls" to keep lower-ranking males out of their vicinity (Galdikas, 1979). These calls are effective at signaling the dominant males' location to females and keeping lower-ranking males at bay; however they will actually attract fellow dominant males, who presumably arrive to displace the calling male. The rare male orangutan interaction consists of intense physical aggression over social ranking and/or a desired mate (Mitani, 1990). Like male orangutans, mountain gorillas are considered to have a one-male mating system (Harcourt, 1981). Most males do not have to engage in male competition with other resident males for fecund females; physical aggression occurs in encounters with out-group males and to prevent local females from joining a different group (Sicotte, 1993). Still, around 40% of mountain gorilla groups are multi-male (Weber & Vedder, 1983). These males may benefit from

the numerical advantage in forming coalitions against out-group males and lower rates of infanticide caused by other adult males (Robbins, 1995). In two multi-male groups, a social dominance hierarchy formed and dominant males accounted for 83% of the observed matings (Robbins, 1999). Aggressive behaviors between male mountain gorillas include grunting, screaming, chest beating, hits, kicks, and bites (Harcourt et al., 1993; Robbins, 1999).

Among bonobos and (common) chimpanzees, our closest living primate relatives, we see many parallels to human social behavior related to male competition. In chimpanzees there are cases of both inter-group and intra-group male aggression and killings (Boesch, Head, Tagg, Arandjelovic, Vigilant, & Robbins, 2007; Fawcett & Muhumuza, 2000). Male chimp coalitions systematically raid neighboring territories, killing the resident males and expanding into their territories (Mitani, Watts, & Amsler, 2010). Larger male bands control more female territories. As chimpanzees form social groups to protect themselves from out-group members, intra-group killings are extremely rare and may be a result of extreme intrasexual competition among males (Wilson & Wrangham, 2003). For example, Fawcett and Muhumuza (2000) documented intra-group male members killing another male in their cohort when the number of cycling females was extremely low. Both wild (Hill, Boesch, Goodall, Pusey, Williams, & Wrangham, 2001; Goodall, 1986; Nishida, 1990) and captive chimpanzee populations (Dyke, Gage, Alford, Swenson, & Williams-Blangero, 1995) have higher male than female mortality rates.

Bonobos are notable for being a peaceful species with very little violence or overt intrasexual competition (de Waal & Lantig, 1988). Bonobos form matrilineal groups with strong female alliances that may have led to low levels of aggression and sexual coercion (Wrangham, 1993). Yet male-male aggression

increases in frequency and intensity on mating days and corresponds to the number of estrous females, and the aggressors mated more often than their targets (Hohmann & Fruth, 2003).

Humans are much less polygynous in comparison to most other primates, but the vast majority of cultures (84% of those documented by anthropologists) allow for polygynyous relationships (Ember, Ember, & Low, 2007) and the variation in male reproductive success is substantially higher than in female reproductive success. Women favor men with abundant access to resources and phenotypic cues of gene quality (Gangestad & Thornhill, 1997; Lancaster, 1989; Buss & Schmitt; 1993). Because a few males gain a disproportionately high number of matings, male mating competition is a potent selection force (Betzig, 1986). The degree of physical sexual dimorphism is directly related to the level of male mating competition (see Bribiescas, 2006), and human females are on average 80% as large as males (Clutton-Brock, 1985).

Proximate Causation

Sexual selection has resulted in a variety of human sex differences in psychology and behavioral tendencies related to mortality, including the greater male tendencies for risk-taking, competitiveness, aggression, and sensitivity to position in social hierarchies (Cronin, 1991). This accounts for many of the immediate causal mechanisms within and outside the individual for sex divergent mortality patterns. Mating competition among men includes potentially lethal violence in conflicts both within and between groups (Chagnon, 1988). Archeological evidence indicates that a much higher proportion of individuals died from violent acts than those in modern societies (e.g., Schulting, 2006). Foraging societies frequently feature opportunistic raiding and ambushes, which are more common than organized formal battles (Buss, 1995; Ember, 1978; Keeley, 1996). These conflicts emerge from motives to retaliate for

previous killings, acquire resources, elevate personal prestige, and acquire women. Yanomamo men who have killed have higher social status and more wives than those who have not, thus about 40% have killed other men (Chagnon, 1988). Violent inter-tribal conflict long preceded the arrival of Europeans in the Americas. Around 1325 CE, half a thousand individuals died violently in a single incident in the Dakotas and none of the remains found were of young women (Keeley, 1996). In contrast to contemporary fictive depictions, warfare is typically less frequent in tribal groups after contact with modern societies (Keeley, 1996).

Human mortality patterns and sex differences in mortality rates have been influenced by numerous historical factors. In about the past 10,000 years, the rise of agriculture and domestication of animals led to higher mortality rates from infectious diseases, facilitated by increasing population size and density, increased mobility, and the greater prevalence of pathogens transferred from other animals (Diamond, 1997). In the last two centuries, modern public health and sanitation measures, vaccination, antibiotics, and other features of scientific medicine have resulted in a major epidemiological transition from mortality mainly caused by infection, other acute diseases and pregnancy and childbirth, to mortality resulting mainly from chronic diseases related to lifestyle and aging in technologically advanced nations (Lopez, 1998). As the massive and relatively sex indiscriminate death rates from infection decline, and as deaths from childbirth decrease, mortality discrepancies arising from behavioral causes become proportionately much more prominent (Kruger & Nesse, 2004). Technological innovations in transportation, weaponry, and manufacturing have exacerbated sex differences in mortality from risky behaviors. The proportionate contribution of causes of death mediated by health related behaviors, such as smoking and poor diet, has also increased sex differences in

mortality in middle and late adulthood (Kruger & Nesse, 2004). In many countries, this secondary peak reached its highest levels a few decades ago and is gradually declining (Kruger & Nesse, 2004), perhaps from historical reductions sex differences in rates of health impacting risky behaviors such as tobacco smoking. Overall, the discrepancy between male and female mortality rates steadily increased in developed nations across the twentieth century (Kruger & Nesse, 2004; Lopez, 1998; Zhang, Sasaki, & Kesteloot, 1995).

We consider the ratio of male to female mortality rates to be a useful indicator reflecting the interaction of evolved strategies and socio-environmental conditions. Thus, we utilize the Male:Female Mortality Ratio (M:F MR) in our descriptive results, as it efficiently indicates population characteristics such as the severity of male-male competition, environmental uncertainty, and the degree of variance in resources and social status. In the contemporary USA, cardiovascular disease accounts for the single greatest proportion (26%) of excess male life years lost beyond female mortality rates. External causes account for 35% of excess male life years lost, including non-automobile accidents (10%), suicide and auto-accidents (both 9%), and homicide (7%). Malignant neoplasms (cancer) account for 8%, liver disease and cirrhosis 3%, congenital abnormalities 2%, and cerebrovascular disease (stroke), pneumonia & influenza, and diabetes mellitus each account for 1% (Kruger, & Nesse, 2004). The remainder of causes account for approximately 23% of excess male life years lost; however all individual causes account for less than 1%.

Multiple levels of proximate factors influence mortality risk. Humans share the XX/XY sex-determination system with most other mammals. The Y-chromosome in males is considerably shorter than the X chromosome and contains an incomplete set of alleles. Thus, males are more susceptible to harmful mutations on the X chromosome because there are less likely to have the normal counterpart (Smith & Warner, 1989). Whereas female sex hormones appear to have beneficial physiological influences (Lawlor, Ebrahim, & Smith, 2001), testosterone has a detrimental impact on many somatic systems (Folstad & Karter, 1992; Hazzard, 1990). Male secondary sexual characteristics are dependent on testosterone levels; this dynamic represents a trade-off between reproductive and somatic investment. Males are more vulnerable to infection and parasites because of the interference of testosterone with immunological systems (Hazzard, 1990; Kraemer, 2000; Moore & Wilson, 2002). High ranking chimpanzee males have both higher testosterone levels and increased parasite burden.

(Muehlenbein & Watts, 2010). Male New Zealand fur seals who facilitate mating by establishing territories also have both higher testosterone levels and increased parasite burden compared to non-territorial males; territorial males show both more aggressive behavior with other males and more sexual behavior with females in this moderately polygynous species (Negro, Caudron, Dubois, Delahaut, & Gemmell, 2010). Larger male body size also poses greater physiological costs (Owens, 2002). Increased dietary fat consumption has led to epidemic cardiovascular disease in Western Nations in recent decades. This has disproportionately affected men in part because they are more susceptible to atherosclerosis at any given level of fat intake (Lawlor, Ebrahim, & Smith, 2001).

Epidemiologists are beginning to recognize the evolutionary origins of riskier male behavior in their recommendations for health-promoting interventions (e.g., Nell, 2002). Men consume greater amounts of alcohol than women, contributing to substantially higher mortality from chronic liver disease and cirrhosis (Zhang, Sasaki, & Kesteloot, 1995). Men also smoke more tobacco than women, though the sex

differential in mortality for lung cancer and stroke is declining because of decreases in male smoking rates (Lopez, 1998) as well as increases in female smoking rates (Pampel, 2002). Males die at higher rates from motor vehicle accidents, even accounting for sex differences in the number of miles driven (Jonah, 1986). Males also have much higher rates of death from violent behaviors (Daly & Wilson, 1997; Kraemer, 2000) and suicides (McClure, 2000). Occupational hazards increase mortality in disproportionately male professions (Hazzard, 1986).

Male tendencies for riskier behavioral patterns are ultimately a result of greater skew and variance in reproductive success compared to females. Wilson and Daly (1997) argue that this risk taking and discounting of future prospects could be a rational response to uncertainty in outcomes. They propose a convex-upward association between proximate outcomes of risk-taking (e.g., social status, resource control, mating opportunities) and reproductive success in unpredictable environments. Thus, these tendencies are maintained in the population because they provided sufficient reproductive benefits to some proportion of individuals to be, even if they are also detrimental to many individuals.

Developmental Ontogeny

Human males are usually at greater risk of mortality at all stages of life. Pregnancies with male fetuses have higher miscarriage rates than those for females (MacDorman, Hoyert, Martin, Munson, & Hamilton, 2007). A male fetus will typically extract more resources from the mother to grow larger than females, leading to greater risks of pre-mature labor. Campbell (2005) argues that behavioral sex differences in childhood reflect preparation for the male status contests of adolescence. Boys are more assertive than girls at only a year and one month old (Goldberg & Lewis, 1969) and boys between 2 and 4 are more aggressive and destructive towards people and objects than

girls (Koot & Verhulst, 1991). Rough and tumble play is three to six times more frequent in boys than girls, consisting of chasing, capturing, wrestling, and restraining (DiPietro, 1981). This form of play appears to be a mechanism for establishing social dominance, something boys consider more important than girls do (Jarvinen & Nicholls, 1996). Male dominance hierarchies emerge at six years of age and relative social status predicts social rank nine years later (Weisfeld, 1999).

Sex differences in mortality from direct behavioral causes increase rapidly during adolescence (Kruger & Nesse, 2004, 2006a), corresponding to the activation of the reproductive neuroendocrine system (Bribiescas, 2006). The steady rise in adrenal androgens initiates the physical transition to adulthood, marking the life history transition from the somatic effort of building and maintaining the body towards reproductive effort. Male mating effort peaks in young adulthood in modern societies, consistent with violent behavioral patterns and injuries from accidents (See Figure 3). Men between ages 20 and 34 are most likely to commit and be the victims of homicide (Daly & Wilson, 1988). Young men may not yet have partners or offspring to invest in and thus can devote more effort to mating, and they may also be more attractive to females because they have not committed their resources (Hill & Kaplan 1999). Among Ache foragers, younger men fathered more children through extra-pair copulations than older men, who fathered more children through long-term relationships (Hill & Hurtado 1996).

In Western industrialized countries, male testosterone levels peak just after age 20, declining gradually until more rapid drops after age 40. Marriage leads to declines in testosterone, though levels increase following divorce (Mazur & Michalek, 1998), reflecting shifting life history. Men who grew up in working-class families during New Zealand's

widespread unemployment of the 1980s and 1990s had low expectations for their futures and made little effort to build job skills or integrate with mainstream society - affiliating with anti-social cohorts and engaging in frequent use of alcohol and other drugs. However, these men generally become more pro-social, economically productive, and family oriented after having children (Rouch, 2010).

Life history patterns may differ somewhat in non-industrialized populations, where testosterone does not decline as rapidly in later adulthood (Ellison, Bribiescas, Bentley, Campbell, Lipson, Panter-Brick, & Hill, 2002). Among the Ache, for example, sex differences in mortality remain high throughout adulthood (Kruger & Nesse, 2006a). The forest dwelling Ache had a flexible social system allowing for

easy remarriage and most adult women had children by several different fathers. Organized club fighting gave women opportunities to evaluate mates and new partnerships would often begin after club fights (Hill & Hurtado, 1996).

Cardiovascular disease was apparently absent in the forest dwelling Ache (Hill & Hurtado, 1996). In industrialized countries, sex differences for behaviorally moderated internal causes peak in mid to late adulthood, consistent with the lag in the impact of health-related behaviors on mortality (Kruger & Nesse, 2004, 2006a). Internal causes of death comprise both the largest source of mortality and the predominant proportion of life years lost from excess male mortality in middle to late adulthood (See Figure 4).

Figure 3. *Male:Female Mortality Ratios in The USA For External Causes During The Year 2000 (From Kruger & Nesse, 2004).*
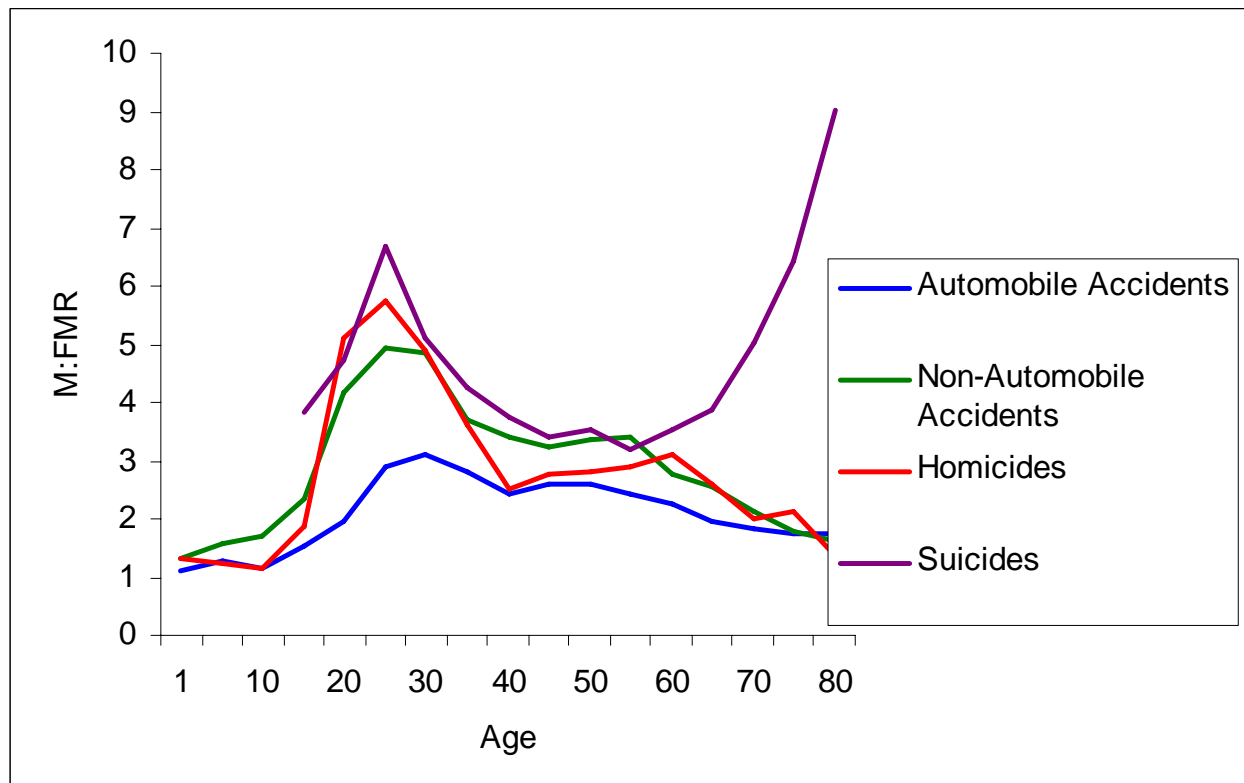

Environmental conditions, broadly defined, influence the magnitude of sex differences in

mortality. Social norms for boys to be tough and to not express emotions such as anxiety

and shame may encourage risky male behavior (Kindlon & Thompson, 1999; Kraemer, 2000). Environmental uncertainty is associated with riskier behavioral strategies, as opportunities may be unpredictable and fleeting (Chisholm, 1999; Figueredo, Vásquez, Brumbach, Sefcek, Kirsner, & Jacobs, 2005; Roff, 1992; Stearns, 1992). Neighborhood life expectancy predicts homicide rates, controlling for the impact of homicide (Wilson & Daly, 1997). Risk taking was higher among those who had lower lifespan expectations and perceived future events as less predictable (Hill, Ross, & Low,

1997). In environments with high pathogen load, where parenting cannot improve offspring survival, male strategies place more emphasis on mating effort including greater risk taking and violence (Quinlan, 2007). Men with relatively low social status and resources may adopt risky strategies, having less to lose and facing the historical price of failure in evolutionary terms. In the United States, sex differences in mortality rates are higher among those lower in income and education (Kruger & Nesse, 2006a).

Figure 4. *Male:Female Mortality Ratios in the USA for internal causes during the year 2000 (From Kruger & Nesse, 2004).*
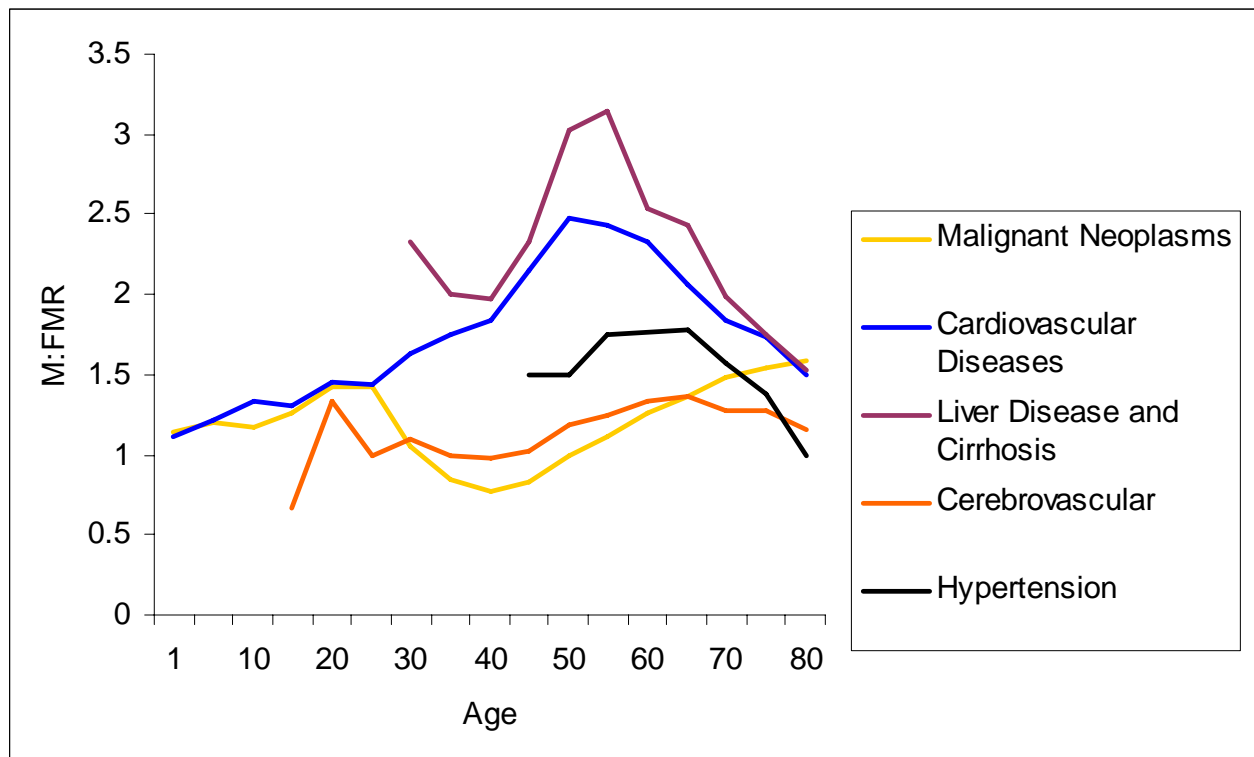
The death rate from assaults is an order of magnitude more prevalent in Scottish routine laborers than managers and professionals (Leyland & Dundas, 2010). Children growing up in poverty are exposed to more violence (Sampson & Lauritsen, 1994), and this exposure is associated with individuals' tendencies for violent behavior (Salzinger, Feldman,

Stockhammer, & Hood, 2002). The extent of neighborhood poverty explained over two-thirds of the variance in violent crime in one Census Tract level study (Coulton, Korbin, Su, & Chow, 1995). Across history, men who had dim prospects otherwise became warriors, adventurers, and explorers (Daly & Wilson, 1988; Daly & Wilson, 2001).

The degree of inequality in outcomes historically related to male reproductive success will drive male competition and sex differences in mortality. Neighborhood income inequality predicts homicide rates (Wilson & Daly, 1997) and modern societies with greater degrees of economic inequality have disproportionately higher levels of male mortality (Kruger, 2010). Consistent with patterns observed across species, the degree of polygyny (indicating male reproductive inequality) is also associated with the degree of excess male mortality. Across nations, these two factors explain the majority of the variance in sex differences in mortality rates (Kruger, 2010). In addition, a relative population surplus of men increases mortality risk for men, but not women (Jin, Elwert, Freese, & Christakis, 2010).

Changes in environmental conditions associated with the intensity of male mating competition can influence sex differences on a relatively short time scale. The variance and skew in social status and resources in Eastern Europe rose sharply during the rapid transition market economies in the 1990s (United Nations Development Program, 1998). Sex differences in mortality rates increased substantially for most of these nations, most prominently during early adulthood, especially compared trends in Western European countries during this period (See Figure 5; Kruger & Nesse, 2007). During the Croatian War of Independence in 1991-1995, evolved facultative adaptations responding to adverse and unstable environments apparently led to riskier behavioral strategies in the civilian population. Sex differences in non-war related violence and accidents peaked one year after the military conflict climaxed in intensity and the non-war male homicide rate was considerably higher for several years following the conflict compared to before (Kruger & Nesse, 2006b).

Figure 5. *Male: Female Mortality Ratios across the Eastern European Economic Transition.*
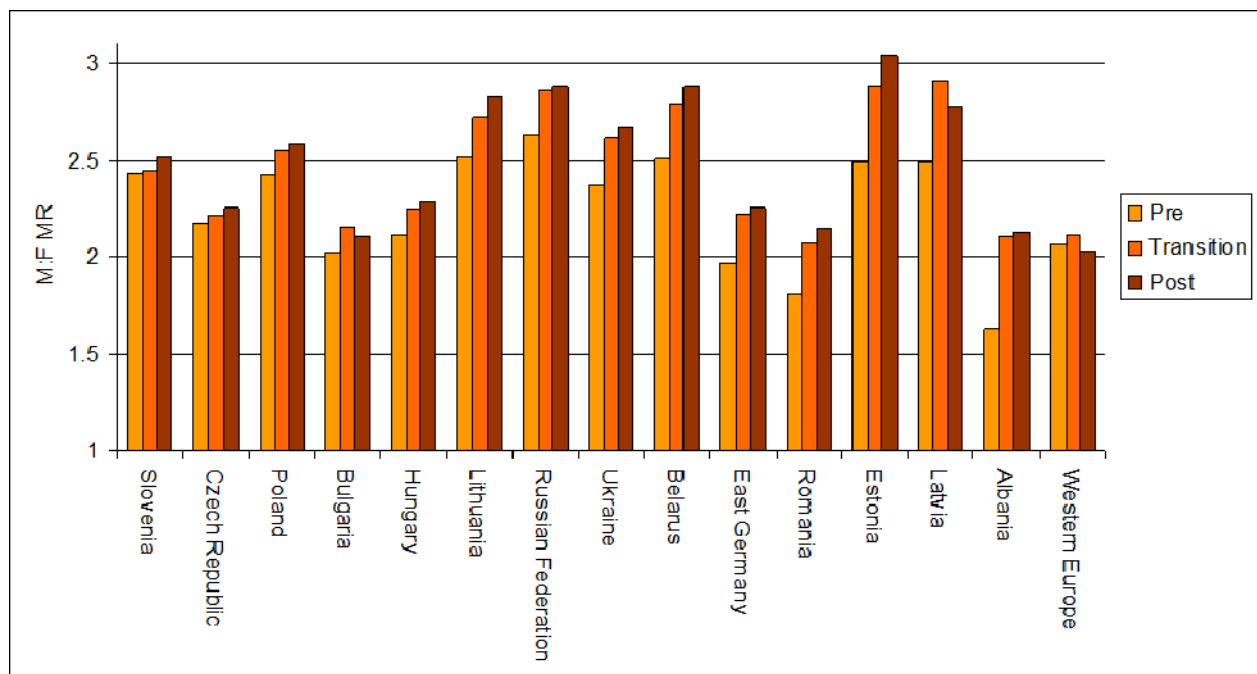
Note: *Pre-Transition 1985-89, Transition 1990-94, Post-Transition 1995-1999 (From Kruger & Nesse, 2007).*

Conclusion

Tinbergen's Four Questions serve as a powerful framework for building a comprehensive understanding of sex differences in human mortality rates. They inherently and explicitly address many of the common misunderstandings of evolutionary explanations for human behavior and its consequences. The respective roles of proximate psychological mechanisms that facilitate adaptive behavior, social and cultural conditions influencing tendencies, and evolutionary selection pressures are clearly outlined, quashing confusions over these issues for careful readers. Cross-species comparisons illustrate how factors related to reproductive dynamics influence mortality patterns in predictable ways. Comparisons of groups within a society, associations between societies, and trends in societies undergoing theoretically relevant changes in conditions provide converging evidence. The development of behaviors across the lifespan and environmental influences shaping behavior complete the depiction of the causal framework. All evidence converges on the intensity of male mating competition as the crucial factor in predicting the degree to which males face greater mortality risk than females. Sex differences in mortality patterns emerge from the basic properties of sexual reproduction and co-vary with other important life history attributes both across species and within human populations.

Evolutionary theory is the most powerful explanatory system in the life sciences and is the only framework that can unify knowledge in otherwise disparate fields of research. Scholars of social and health issues and practitioners intervening with individuals and larger scales of organization would benefit considerably from an understanding of the basic principles of evolution and its consequences for humans. The eventual integration of evolutionary principles will gradually enhance the effectiveness of health interventions and provide an ultimate explanation for otherwise puzzling patterns in health outcomes. Tinbergen's framework may accelerate the pace of this integration through its holistic explanatory utility.

References

Alberts, S. C., Watts, H. E., & Altmann, J. E. (2003). Queuing and queue-jumping: Long-term patters of reproductive skew in male savannah baboons, *papio cynocephalus*. *Animal Behaviour, 65*, 821-840.

Bateman, A. J. (1948). Intra-sexual selection in *drosophila*. *Heredity, 2*, 349-368.

Bell, G. (1982). *The masterpiece of nature: The evolution and genetics of sexuality*. London: CroomHelm.

Betzig, L. (1986). *Despotism and differential reproduction: A Darwinian view of history*. Hawthorne, NY: Aldine de Gruyter.

Boesch, C., Head, J., Tagg, N., Arandjelovic, M., Vigilant, L., & Robbins, M. M. (2007). Fatal chimpanzee attack in Loango National Park, Gabon. *International Journal of Primatology, 28*, 1025-1034.

Bribiescas, R. G. (2006). *Men: Evolutionary and Life History*. Cambridge, MA: Harvard University Press.

Bulger, J. B. (1993). Dominance rank and access to estrous females in male savanna baboons. *Behaviour, 127,* 67–103.

Bulmer, M. G., & Parker, G. A. (2002). The evolution of anisogamy: A game-theoretic approach. *Proceedings of the Royal Society of London, Series B, 269,* 2381–2388.

Buss, D. M. (1989). Sex difference in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioural and Brain Sciences, 12*, 1-49.

Buss, D. M. (2005). *The murderer next door: Why the mind is designed to kill*. New York: Penguin Press.

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review, 100*, 204-232.

Campbell, A. (1999). Staying alive: Evolution, culture, and women's intrasexual aggression. *Behavioural and Brain Sciences, 22*, 203-252.

Chagnon, N. A. (1992). *Yanomamo*. New York: Holt, Rinehart, & Winston.

Chisholm, J. S. (1999). *Death, hope and sex: Steps to an evolutionary ecology of mind and morality*. Cambridge, UK: Cambridge University Press.

Clutton-Brock, T. H. (1985). Size, sexual dimorphism and polygamy in primates. In W. L. Jungers (Ed.), *Size and scaling in primate biology* (pp. 211-237). New York: Plenum.

Clutton-Brock, T. H., & Isvaran, K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society of London, Series B*: *Biological Sciences*, 274, 3097-3104.

Coulton, C., Korbin, J., Su, N., & Chow, J. (1995). Community level factors and child maltreatment rates. *Child Development, 66,* 1262-1276.

Cronin, H. (1991). *The ant and the peacock: Altruism and sexual selection from Darwin to today*. New York: Cambridge University Press.

Daly, M., & Wilson, M. (1978). *Sex, evolution, and behavior: Adaptations for reproduction*. North Scituate, MA: Duxbury Press.

Daly, M. & Wilson, M. (1988). *Homicide*. New York: Aldine de Gruyter.

Daly, M. & Wilson, M. (1997). Crime and conflict: Homicide in evolutionary perspective. *Crime and Justice, 22,* 251-300.

Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: Murray.

Dawkins, R. (1976). *The selfish gene*. New York: Oxford University Press.

de Waal, F. B. M., & Lantig, F. (1998). *Bonobo: The forgotten ape.* Berkeley and Los Angeles, CA: University of California Press.

Diamond, J. (1997). *Guns, germs, and steel: The fates of human societies* (1st ed.). New York: W. W. Norton.

DiPietro, J. A. (1981). Rough and tumble play: A function of gender. *Developmental Psychology, 17,* 50-58.

Dyke, B., Gage, T. B., Alford, P. L., Swenson, B., & Williams-Blangero, S. (1995). Model life table for captive chimpanzees. *American Journal of Primatology, 37,* 25-37.

Ellison, P. T., Bribiescas, R. G., Bentley, G. R., Campbell, B. C., Lipson, S. F., Panter-Brick, C., & Hill, K. (2002). Population variation in age-related decline in male salivary testosterone. *Human Reproduction, 17,* 3251-3253.

Ember, C. R. (1978). Myths about hunter-gatherers. *Ethnology, 17,* 439-448.

Ember, M., Ember, C. R., & Low, B. S. (2007). Comparing explanations of polygyny. *Cross-Cultural Research, 41,* 428-440.

Fawcett, K., & Muhumuza, G. (2000). Death of a wild chimpanzee community member: Possible outcome of intense sexual competition. *American Journal of Primatology, 51,* 243-247.

Figueredo, A. J., Vásquez, G., Brumbach, B. H., Sefcek, J. A., Kirsner, B. R., & Jacobs, W. J. (2005). The K-Factor: Individual differences in life history strategy. *Personality and Individual Differences, 39,* 1349–1360.

Folstad, I. & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist, 139,* 603-622.

Galdikas, B. (1979). Orangutan adaptation at Tanjung Puting Reserve: Mating and ecology. In D. Hamburg & E. McCown (Eds.), *The Great Apes* (pp. 194-233). Menlo Park, CA: Benjamin Cummings.

Gangestad, S. W., & Thornhill, R. (1997). Human sexual selection and developmental stability. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary Social Psychology* (pp. 169-195). Mahwah, NJ: Erlbaum.

Goldberg, S., & Lewis, M. (1969). Play behavior in the year-old infant: Early sex differences. *Child Development, 40,* 21-31.

Goodall, J. (1986). *The chimpanzees of Gombe*. Boston: Houghton Mifflin Publishing.

Harcourt, A. H. (1981). Intermale competition and the reproductive behavior of the great apes. In C. E. Graham (Ed.), *Reproductive Biology of the Great Apes* (pp. 301–318). New York: Academic Press.

Harcourt, A. H., Stewart, K. & Hauser, M. (1993). Functions of wild gorilla 'close' calls. I. Repertoire, context, and interspecific comparison. *Behaviour, 124,* 91–122.

Harvey, P. H. & Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution, 39,* 559-581.

Hazzard, W. (1986). Biological basis of the sex differential in longevity. *Journal of the American Geriatrics Society, 34,* 455-471.

Hazzard, W. (1990). The sex differential in longevity. In Hazzard, W., Endres, R., Bierman, E. and Blass, J. (Eds.), *Principles of Geriatric Medicine and Gerontology.* (2nd ed., pp. 37-47). New York: McGraw Hill.

Hill, E. M., Ross, L. T. & Low, B. S. (1997). The role of future unpredictability in human risk-taking. *Human Nature, 8,* 287-325.

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J. & Wrangham, R. (2001). Mortality rates among wild chimpanzees. *Journal of Human Evolution, 40,* 437–450.

Hill, K., & Hurtado, M. (1996). *Ache life history: The ecology and demography of a foraging people.* Hawthorne, NY: Aldine de Gruyter.

Hill, K., & Kaplan, H. (1999). Life history traits in humans: Theory and empirical studies. *Annual Review of Anthropology, 28,* 397-438.

Hohmann, G., & Fruth, B. (2003). Intra- and inter-sexual aggression by bonobos in the context of mating. *Behaviour, 140,* 1389-1413.

Hopcroft, R. L. (2006). Sex, status and reproductive success in the contemporary U.S. *Evolution and Human Behavior, 27*, 104-120.

Hrdy, S. B. (1977). *The langurs of Abu: Female and male strategies of reproduction.* Cambridge, MA: Harvard University Press.

Jarvinen, D. W. & Nicholls, J. G. (1996). Adolescents' social goals, beliefs about the causes of social success and dissatisfaction in peer relations. *Developmental Psychology, 32,* 435-441.

Jin, L., Elwert, F., Freese, J., & Christakis, N. A. (2010). Preliminary evidence regarding the hypothesis that the sex ratio at sexual maturity may affect longevity in men. *Demography, 47,* 579-586.

Jonah, B. A. (1986). Accident risk and risk-taking behavior among young drivers. *Accident Analysis & Prevention, 18,* 255-271.

Jordan, L. A., & Brooks, R. C. (2010). The lifetime costs of increased male reproductive effort: courtship, copulation and the Coolidge effect. *Journal of Evolutionary Biology, 23,* 2403-2409.

Kaplan, H., & Hill, K. (1985). Hunting ability and reproductive success among male Ache foragers. *Current Anthropology, 26,* 131-133.

Keeley, L. H. (1996). *War before civilization.* New York: Oxford University Press.

Kindlon, D., & Thompson, M. (1999). *Raising Cain: Protecting the emotional life of boys.* London: Michael Joseph.

Kirkwood, T. B., and Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 332,* 15-24.

Koot, H. M. & Verhulst, F. C. (1991). Prevalence of problem behavior in Dutch children aged 2-3. *Acta Psychiatricia Scandinavica, 83,* 1-37.

Kraemer, S. (2000). The Fragile Male. *British Medical Journal, 321,* 1609-12.

Kruger, D. J. (2010). Socio-demographic factors intensifying male mating competition exacerbate male mortality rates. *Evolutionary Psychology, 8,* 194-204.

Kruger, D. J., & Nesse, R. M. (2004). Sexual selection and the Male:Female Mortality Ratio. *Evolutionary Psychology, 2,* 66-77.

Kruger, D.J., & Nesse, R. M. (2006a). An evolutionary life-history framework for understanding sex differences in human mortality rates. *Human Nature, 17,* 74-97.

Kruger, D. J., & Nesse, R. M. (2006b). Understanding sex differences in Croatian mortality with an evolutionary framework. *Psychological Topics, 15,* 351-364.

Kruger, D.J., & Nesse, R. M. (2007). Economic transition, male competition, and sex differences in mortality rates. *Evolutionary Psychology, 5,* 411-427.

Kuester, J., & Paul, A. (1992). Influence of mate competition and female choice on male mating success in Barbary macaques. *Behaviour, 120,* 192-217.

Lancaster, J. B. (1989). Evolutionary and cross-cultural perspectives on single-parenthood. In R. W. Bell & N. J. Bell (Eds.), *Interfaces in Psychology* (pp. 63-72). Lubbock, TX: Texas Tech University Press.

Lawlor, D.A., Ebrahim, S., & Smith, G.D. (2001). Sex matters: Secular and geographical trends in sex differences in coronary heart disease mortality. *British Medical Journal, 323,* 541-545.

Leutenegger, W., and Kelly, J. T. (1977). Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates, 18,* 117-136.

Leyland, A. H., & Dundas, R. (2010). The social patterning of deaths due to assault in Scotland, 1980–2005: population-based study. *Journal of Epidemiology and Community Health, 64,* 432-439.

Lopez, A. D. (1998). Morbidity and mortality, changing patterns in the twentieth century. In P. Armitage and T. Colton (Eds.). *Encyclopedia of biostatistics* (pp. 2690-2701). New York: John Wiley and Sons.

Low, B. (1998). The Evolution of Human Life Histories. In C. Crawford and D. Krebs, (Eds.), *Handbook of evolutionary psychology: Issues, ideas, and applications* (pp. 131-161). Mahwah, NJ: Lawrence Erlbaum Associates.

Low, B. (2003). Ecological and social complexities in monogamy. In U. Reichard and C. Boesch (Eds.), *Monogamy: Mating strategies and partnerships in*

birds, humans, and other mammals (pp. 161-176). Cambridge, UK: Cambridge University Press.

Low, B. (2007). Ecological and socio-cultural impacts on mating and marriage systems. In R. Dunbar and L. Barrett (Eds.), *The Oxford handbook of evolutionary psychology* (pp. 449-462). Oxford, UK: Oxford University Press.

MacDorman, M.F., Hoyert, D.L., Martin, J.A., Munson, M.L., & Hamilton, B.E. (2007). Fetal and perinatal mortality, United States, 2003. *National Vital Statistics Reports, 55*(6), 1-18.

Mazur, A., & Michalek, J. (1998). Marriage, divorce, and male testosterone. *Social Forces, 77,* 315–330.

Medawar, P. B. (1952). *An unsolved problem of biology*. London: H.K. Lewis.

Miller, G. F. (1998). How mate choice shaped human nature: A review of sexual selection and human evolution. In C. Crawford & D. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 87-129). Mahwah, NJ: Lawrence Erlbaum.

Mitani, J. C. (1990). Experimental field studies of Asian ape social systems. *International Journal of Primatology, 11,* 103-126.

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology, 20,* R507-508.

McClure, G. (2000). Changes in suicide in England and Wales, 1960-1997. *British Journal of Psychiatry, 176,* 64-67.

Møller, A. P., Christe, P. & Lux, E. (1999). Parasitism, host immune function, and sexual selection. *Quarterly Review of Biology, 74,* 3–20.

Moore, S. L., & Wilson, K. (2002). Parasites as a viability cost of sexual selection in natural populations of mammals. *Science, 297,* 2008-2009.

Muehlenbein, M.P., & Watts, D.P. (2010). The costs of dominance: testosterone, cortisol and intestinal parasites in wild male chimpanzees. *BioPsychoSocial Medicine, 4*:21.

Negro, S. S., Caudron, A. K., Dubois, M., Delahaut, P., & Gemmell, N. J. (2010). Correlation between male social status, testosterone levels, and parasitism in a dimorphic polygynous mammal. *PLoS ONE, 5:*9.

Nell, V. (2003). Why young men drive dangerously: Implications for injury prevention. *Current Directions in Psychological Science, 11,* 75-79.

Nishida, T. (1990). *The chimpanzees of the Mahale mountains*. Tokyo: University of Tokyo Press.

Owens, I. P. F. (2002). Sex Differences in Mortality Rate. Science, 297, 2015-2018.

Pampel, F. (2002). Cigarette Use and the Narrowing Sex Differential in Mortality. *Population and Development Review, 28,* 77-104.

Plavcan, J. M. (2000). Inferring social behavior from sexual dimorphism in the fossil record. *Journal of Human Evolution, 39,* 327-344.

Plavcan, J. M., & van Schaik, C. P. (1997). Interpreting hominid behavior on the basis of sexual dimorphism. *Journal of Human Evolution, 32,* 345-374.

Plavcan, J. M., van Schaik, C. P., & Kappeler, P. M. (1995). Competition, coalitions and canine size in primates. *Journal of Human Evolution, 28,* 245-76.

Promislow, D. E. (1992). Costs of sexual selection in natural populations of mammals. *Proceedings of the Royal Society of London, Series B, 247,* 230-210.

Quinlan, R.J. (2007). Human parental effort and environmental risk. *Proceedings of the Royal Society of London, Series B, 274,* 121-125.

Reichard, U., & Boesch, C. (2003). *Monogamy: Mating strategies and partnerships in birds, humans, and other mammals*. Cambridge, UK: Cambridge University Press.

Robbins, M. M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour, 132,* 21–47.

Roff, D. A. (1992). *The evolution of life histories: Theory and analysis.* New York: University of Chicago Press.

Rogers, R. G., Hummer, R. A. & Nam, C. B. (2000). *Living and dying in the USA: Behavioral, health, and social differences of adult mortality*. San Diego, CA: Academic Press.

Rouch, G. (2010). Fatherhood and family life: Securing low-skilled/low-paid men within the margins of society. *Institute of policy studies working paper 10/07*. Wellington, NZ: Victoria University of Wellington School of Government.

Salzinger, S., Feldman, R. S., Stockhammer, T., & Hood, J. (2002). An ecological framework for understanding risk for exposure to community violence and the effects of exposure on children and adolescents. *Aggression and Violent Behavior, 7,* 423-451.

Sampson, R. J., & Lauritsen, J. (1994). Violent victimization and offending: Individual, situational and community-level risk factors. In A. J. Reiss & J. A. Roth (Eds.), *Understanding and preventing violence: Social influences* (vol. 3, pp. 1-114). Washington, DC: National Academy Press.

Schulting, R. J. (2006). Skeletal evidence and contexts of violence in the European Mesolithic and Neolithic. In R. Gowland and C. Knüsel (Eds.), *The*

social archaeology of funerary remains (pp. 224-237). Oxford, UK: Oxbow Books.

Sicotte, P. (1993). Inter-group encounters and female transfer in mountain gorillas: Influence of group composition on male behavior. *American Journal of Primatology, 30,* 21-36.

Smith, D. W., & Warner, H. R. (1989). Does Genotypic Sex have a Direct Effect on Longevity. *Experimental Gerontology, 24,* 277-288.

Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X. & Takenaka, O. (1997). Sexual selection in Japanese macaques II: Female mate choice and male-male competition. *Animal Behaviour, 54,* 737-746.

Stearns, S. C. (1992). *The evolution of life histories.* Oxford: Oxford University Press.

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review, 107,* 411-429.

Tinbergen, N. (1963) On aims and methods in ethology. *Zeitschrift für Tierpsychologie, 20,* 410–433.

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man: 1871-1971* (pp. 136-179). Chicago: Aldine.

United Nations Development Program, Regional Bureau for Europe and the CIS (1998). *Poverty in transition?* New York: Author.

Weber, A. W., & Vedder, A. (1983). Population dynamics of the Virunga gorillas: 1959-1978. *Biological Conservation, 26,* 341-366.

Weisfeld, G. E. (1999). *Evolutionary principles of human adolescence*. New York: Basic Books.

Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution, 11,* 398-411.

Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press.

Williams, G. C. (1975). *Sex and Evolution*. Princeton, NJ: Princeton University Press.

Wilson, M. & Daly, M. (1985). Competitiveness, Risk Taking, and Violence: The Young Male Syndrome. *Ethology and Sociobiology, 6,* 59-73.

Wilson, M., & Daly, M. (1993). Lethal confrontational violence among young men. In N. J. Bell and R. W. Bell (Eds.), *Adolescent Risk Taking* (pp. 84–106). Newbury Park, California: Sage Publications.

Wilson, M., & Daly, M. (1997). Life expectancy, economic inequality, homicide, and reproductive timing in Chicago neighbourhoods. *British Medical Journal, 314,* 1271-1274.

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology, 32,* 363-392.

Wrangham, R. W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature, 4,* 47-79.

Zhang, X., Sasaki, S., & Kesteloot, H. (1995). The sex ratio of mortality and its secular trends. *International Journal of Epidemiology, 24*, 720-729.

Daniel J. Kruger, Ph.D., is Research Assistant Professor at the School of Public Health and Institute for Social Research at the University of Michigan. He completed his dissertation at Loyola University Chicago in 2001 integrating proximate and ultimate influences for altruistic behaviors. He has published over 50 peer-reviewed scientific articles. His evolutionary research interests include altruism, cooperation, competition, life history, mating strategies, risk taking, and mortality patterns.

Carey J. Fitzgerald, Ph.D., graduated in 2011 from the Applied Experimental Psychology program at Central Michigan University. His research interests include inclusive fitness, inter-group relations, trust, aggression, and mating strategies.