

# 89 Sex Differences and Intrasexual Variation in Competitive Confrontation and Risk Taking: An Evolutionary Psychological Perspective

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## Glossary

**adaptation** An anatomical, physiological, or behavioral attribute of an organism that has been designed by a history of natural selection to achieve some specific function that contributes to the organism's fitness.

**fitness** Fitness is the expected value, in the statistical sense, of a phenotypic design's success in promoting the relative replicative success of its bearer's genes, in competition with their alleles (alternative variants at the same genetic locus), in the environment(s) in which that phenotypic design evolved.

**future discounting** Future discounting is the rate at which one discounts the future; that is, the rate at which the subjective value of future consumption diminishes relative to the alternative of present consumption (or, if you like, the interest rate required to motivate foregoing consumption).

**secondary sexual characteristic** A secondary sexual characteristic is an attribute that differs between the sexes for reasons other than a direct sex-specific role in reproduction.

**sexual selection** Sexual selection is the component of natural selection (the nonrandom differential reproduction of types) that results from differential access to mates and their reproductive labors.

## 89.1 Introduction

We discuss variations in homicide as indicative of variations in competitive risk taking, interpreting prevalent conflict typologies and demographic patterns as reflections of evolved motivational and information-processing mechanisms that function to regulate competitive inclinations and actions. Connections are then drawn to research on future

discounting and impulsivity, on the effects of inequity on violence, and on the bidirectional influences between circulating testosterone (T) levels and social experience. We argue that Darwinian theory, especially sexual selection theory, provides a framework that can both synthesize existing knowledge in these disparate domains and facilitate future discovery.

## 89.2 An Evolutionary Psychological Perspective

Evolutionary psychology is the pursuit of psychological science with explicit consideration of the fact that the psyche is, like the body, a product of evolutionary processes. More specifically, evolutionary psychologists assume that brains and minds are complexly structured as a result of a history of Darwinian selection, and that it is therefore enlightening to view the psyche and its functional components as adaptations.

The proposition that some attribute is an adaptation is a hypothesis about special-purpose design, and the value of such a hypothesis is that it suggests avenues of inquiry. As [Mayr \(1983\)](#) has noted, for example, generating hypotheses about what the heart or lungs or liver are for were essential first steps for investigating their physiology. Similarly, if psychological mechanisms and processes are characterized at an appropriate level of generality, then they too can be assumed to be for something (brightness compensation, memory consolidation, communication, courtship, etc.). In other words, the psychological constituents of human (and nonhuman) nature, like the anatomical and physiological elements thereof, exhibit adaptive design for the solution of particular recurrent problems faced by our ancestors.

Notions about adaptive design inevitably provide direction to the research enterprise. If we suppose, for example, that forgetting (the nonavailability of previously accessible information) constitutes repression of memories whose recall might interfere with effective action, our experimental hypotheses and methods will be very different than if we instead hypothesize that it is primarily an adaptive process of discarding obsolete information that has lost its predictive utility, or that it is merely a nonadaptive by-product of limited capacity. But if psychological research is almost invariably conducted in the shadow of the investigators' assumptions about what components of the brain/mind are for, then it is surely useful to scrutinize those assumptions, rather than letting them remain implicit, and to consider them

in the light of what evolutionary biologists know about the process that creates functional organization in living creatures.

The Darwinian process of natural selection (including sexual selection) is of course the unwitting designer. Selection, systematic differentials in reproduction, and the proliferation of gene copies, is the force that created existing adaptations as solutions to the adaptive problems that were confronted by ancestral generations. Of course, not all aspects of contemporary organisms are adaptations; the colors of our internal organs, for example, have no functional significance in their own right, and are better understood as nonadaptive by-products of other adaptations. However, any complex, functional component of a living creature is almost certain to be an adaptation whose basic architecture and parameters have been shaped by a history of past selection, replicating better than alternatives because it dealt with some challenge better and thus promoted its bearers' fitness better.

Fitness is a technical term that has been used in several slightly different ways in evolutionary biology ([Dawkins, 1982](#)). Our meaning here is the same as its predominant contemporary meaning: the expected value, in the statistical sense, of a phenotypic design's success in promoting the relative replicative success of its bearer's genes, in competition with their alleles (alternative variants at the same genetic locus), in the environment(s) in which that phenotypic design evolved. Because psychological adaptations control behavioral outputs in systematic response to internal and extrinsic situational variables, we may expect that they have evolved to produce responses that are appropriately contingent, on both immediate and developmental timescales, on those aspects of the environment (including social variables) that were statistical predictors of the average fitness consequences of alternative courses of action in the past.

It should be clear from the previous paragraphs that evolutionary psychologists – like behavioral endocrinologists and neuroscientists, but unlike most social scientists – see no distinction in kind between psychological and biological influences and processes. We take it for granted that processes described at a psychological level (e.g., in terms of cognitions or traits or stimulus–response associations) are somehow instantiated in neural and hormonal mechanisms. We are not saying merely that psychological processes are engaged in continual reciprocal causal interactions with the sorts of physiological states and processes that are often referred to as biological influences on

behavior: psychological processes are fundamentally biological processes. It is no surprise to an evolutionary psychologist, for example, that T should have a variety of subtle effects on information processing and behavior, both by virtue of action in the central nervous system itself and by virtue of other peripheral effects, nor that plasma T levels are themselves affected by social experience (see, e.g., McCaul et al. (1992) and Mazur et al. (1992)). Neither is it surprising to learn that an insult that evokes a surge of T in men raised in the honor culture of the US South, where retaliatory aggression is admired, has no such effect on men raised in the North, where retaliatory aggression is not admired (Cohen et al., 1996). It is often the case that psychophysiological adaptations are best characterized in terms of contingent responsiveness not only to immediate circumstances or stimuli but also to the cumulative consequences of experience, and there is no reason why the experiences in question should not include the assimilation and internalization of local cultural norms.

### 89.2.1 Decision-Making Adaptations

Evolutionists routinely model the costs and benefits of alternative decision rules concerning such matters as how many eggs a bird should lay before she starts incubation, or when a plant should stop putting all its energy into growth and start putting some into reproduction. We call these decisions because the organism has sufficient flexibility or plasticity to pursue alternative courses of action (e.g., either to continue growing taller, or else to terminate growth and flower instead), and because the particular course of action that is actually taken is complexly contingent on information available in the environment that imperfectly but usefully predicts relevant future conditions.

To a layperson, this use of the word decisions may sound metaphorical; a real decision is surely the product of deliberation by a conscious, intentional agent! But exactly how such real decisions differ from the thoughtless decision processes made by our peripheral organs, or by a plant, is less clear than it may first appear. Social and cognitive psychologists have shown that people do not necessarily enjoy privileged insight into the determinants of their own decisions, and that the phenomenology of deliberation and reasoned choice is often illusory and reconstructive. A genuine causal determinant of behavioral choice may be surreptitiously manipulated by an experimenter, while both observers and the subjects themselves confidently espouse coherent but manifestly false explanations of

the subjects' choice of action (see, e.g., Nisbett and Wilson (1977), Nisbett and Ross (1980), and Kahneman et al. (1982)). For example, subjects in such experiments provide elaborate esthetic justifications for preferences that are actually governed by manipulated noise levels whose relevance goes unnoticed. Our reason for mentioning these results is not to show that human decision making and the mental procedures underlying it are illogical or dysfunctional; human inference and choice procedures apparently deal with naturalistic inputs very well (Cosmides and Tooby, 1996; Gigerenzer and Todd, 1999; Rode et al., 1999). Our point is simply that neither mental procedures themselves nor their logic and functionality are necessarily transparent to introspection. More generally, the phenomenology of reasoned consideration notwithstanding, we suggest that essentially all decision making necessarily relies on a great deal of inaccessible mental processing by complex devices designed by selection to generate inferences and choices on the basis of partial information and probabilistic cues.

Emotions are crucial, directive components of this complex evolved machinery, despite the popular misconception that emotion is the enemy of reason. This baseless prejudice has even invaded the social sciences (see Daly and Wilson (1997) for criminological examples and a critique of the presumption that emotional arousal during the commission of crimes is an impediment to effective action and that rational choice theories of crime must therefore be wrong). If it were truly the case that fear, anger, jealousy, and other emotional states interfered with our capacity to make decisions that further our interests, then we would have evolved to be affectless zombies. Clearly, we have not, and that very fact is testimony to the functionality of emotional states. More dramatic evidence to this effect is provided by people whose emotional mechanisms are operating abnormally, and who are therefore incapacitated (Nesse, 1990). Thus, rather than being impediments to dispassionate evaluation of alternatives, emotional states are best interpreted as functional operating modes whose specific attributes are design features facilitating effective response to the particular situations that arouse each of them (Nesse, 1990). In this light, an admonition such as "don't get mad, get even" is grounded in confusion; one of the things that "getting mad" exists for is "getting even."

Once the complexity of the psychophysiological machinery generating even our rational choices is recognized, it no longer seems metaphorical to speak of decisions about such things as when to

ovulate, or when to undergo puberty, in the same language that we apply to processes that select among behavioral options. In all these cases, complex, imperfectly understood procedures, involving evolved information-processing machinery, the vestiges of individual experience, and contemporary extrinsic inputs, generate one choice rather than another. True, the deliberative homunculus of folk psychology seems not to be involved in deciding how much you will let your bone calcium be depleted during lactation, but that is not a problem, for he contributes nothing toward a genuine explanation of how you decide anything. Philosophically, evolutionary psychologists are committed materialists and mechanists, even if the mechanisms of which they speak are often characterized as cybernetic abstractions, such as decision rules or algorithms or contingent responsiveness, rather than in terms of identified neural circuitry or chemical titers.

### 89.2.2 Adaptation versus Pathology

Our own research has sought to illuminate the evolutionary psychology of risk acceptance and competition through the window afforded by the epidemiology of lethal violence. It may seem odd to suggest that such behavior can illuminate adaptation. Criminal violence is often ineffectual, and we will argue later that homicide is better seen as an assay of motives whose useful consequences typically fall short of lethality than as an adaptation in its own right. Moreover, violence is sometimes truly pathological: a product of alcohol-induced psychoses, delusions, organic defects, and so forth (see, e.g., Raine (1993), Aarland et al. (1996), and Giancola and Zeichner (1995)). Nevertheless, the popular metaphor whereby violence itself is deemed a social pathology is weak and potentially misleading.

Perhaps because violence is abhorrent, and because it is a popular metaphor to call socially desirable outcomes healthy, violent behavior is often disparaged as sick. But the implication that violence *per se* is pathological is certainly false (Monahan and Splane, 1980; Cohen and Machalek, 1994). Pathologies are failures – due to mishap, senescent decline, or subversion by biotic agents with antagonistic interests – of anatomical, physiological, and psychological entities or processes, reducing their effectiveness in achieving the adaptive functions for which they evolved (Williams and Nesse, 1991; Nesse and Williams, 1994). To assert that violence is a pathology (and not simply that there are

pathologies of violence) is to maintain that it is nothing more than a functionless manifestation of such failures, analogous to a fracture or a delusional psychosis. This cannot be correct, however, because people and other animals possess psychological and physiological machinery that is very clearly designed for the production and regulation of violence.

The evidence on this point is multifaceted. Most importantly, the typical elicitors of violent response are threats to survival and reproductive prospects, and its typical effect is to counter those threats. Animals (including people) react violently to usurpation of essential resources by rivals, and they direct their violence against those rivals (see, e.g., Archer (1988) and Huntingford and Turner (1987)). Moreover, such violent response is adaptively modulated. Behavioral ecologists have analyzed the cost–benefit structure of confrontational violence in terms of factors affecting the expected results of electing to fight and of escalating, and they have found that animals indeed exhibit contingent response to available cues of the probable costs and benefits of alternative actions (see, e.g., Pruett-Jones and Pruett-Jones (1994), Chase et al. (1994), Turner (1994), and Kvarnemo et al. (1995)). These analyses leave little doubt that violence is regulated with sensitivity to its probable consequences (Andersson, 1980; Clutton-Brock and Parker, 1995; Enquist and Leimar, 1990; Oliveira et al., 1998).

In addition to contextual appropriateness, the motivational states that produce violent action entail complex psychophysiological mobilization for effective agonistic action, and they induce postures appropriate for attack and defense. Some anatomical structures function solely or primarily as intraspecific weapons, and these often develop and regress seasonally or in delimited life stages, so that their availability tracks variations in the utility of violent action. Such weaponry is often sexually differentiated, in ways that make sense when one considers sex differences in the intensity of intrasexual competition, as discussed later. There are also neuroanatomical structures and chemical systems that are dedicated to the production of effective violence, and these too are likely to be sexually differentiated (Archer, 1988; Huntingford and Turner, 1987). Moreover, the magnitude of these sex differences in anatomical weaponry and intrasexual aggressive behavior is variable across species, and this variability is systematically related to aspects of the breeding system, especially its average level of polygamy (Daly and Wilson, 1983). All of these facts testify to the potency of Darwinian

selection in shaping the anatomy and psychology of intrasexual aggression.

The misconception that human violence is mere pathology has been reinforced by its contemporary link to disadvantaged backgrounds that include real threats to healthy development, but this link is by no means universal. In face-to-face societies lacking strong central authority, like the foraging societies in which we evolved, violence was a recourse of highly successful men, too, and contributed to their success (see, e.g., [Chagnon \(1988, 1996\)](#) and [Betzig \(1986\)](#)). In modern nation-states, most people no longer rely on their own or their allies' violent capabilities, with the result that violence is indeed relatively often due to psychopathology, but such pathology is in the regulation of violence, not in its existence. Moreover, we must be alert to politically motivated attributions of pathology that serve to trivialize the grievances of the underprivileged. Violent offenders are disproportionately drawn from social strata with scant access to the opportunities and protective state services available to more fortunate citizens, leaving people in self-help circumstances much like those experienced by most of our ancestors. Violence in such circumstances may be deplorable, but it is not obviously a mistake in terms of the perpetrators' self-interest, and even in those people whose violence is counterproductive, the functional organization of its contingent controls remains evident.

### 89.2.3 Sexual Selection and Competition

In 1871, Darwin provided a significant addendum to his 1859 theory of evolution by natural selection: sexual selection. By natural selection, Darwin meant the nonrandom differential reproduction of types as a result of differential success in coping with challenges such as finding food, avoiding predators, and enduring climatic factors. Sexual selection covered the nonrandom differential reproduction of types as a result of differential access to mates and their reproductive labors. Darwin distinguished these two forces because they could sometimes act in opposition, and the distinction could help explain the evolution of attributes that have no apparent survival value. For example, sexual selection has produced conspicuous courtship structures, like the peacock's tail, that enhance mating success but apparently also increase mortality risk.

It is often useful to further partition sexual selection into effects of competition for mates among same-sex rivals versus effects exerted by the preferences of the opposite sex. Darwin noted that in most taxa, including

the mammals, competition for access to mates occurs mainly (or, at least, most conspicuously) among males rather than females, but he could offer no explanation for this pattern. The issue was clarified by [Bateman \(1948\)](#), [Williams \(1966\)](#), and [Trivers \(1972\)](#), who pointed out that if one sex (e.g., males) provides only a minority of the resources necessary for producing viable young, then individuals of this less investing sex can increase their fitness by polygamous mating, and will have a higher ceiling on potential fitness than individuals of the more investing sex, whose fitness will be limited not by access to more mates but by the time and energy costs of raising offspring. Thus, the less investing sex is likely to have a higher fitness variance, as each successful polygamist consigns one or more rivals to unmated status; the less investing sex will therefore be sexually selected to compete for matings, which represent precious opportunities to parasitize the efforts of the sex that invests more. (There are cases, although not among the mammals, in which males are the more investing sex, and aggressive competition for access to mates occurs mainly among females (see, e.g., [Gwynne and Bailey \(1999\)](#)). More recent theorists have argued that sex differences in potential reproductive rate ([Clutton-Brock and Vincent, 1991](#)) or time allocation ([Parker and Simmons, 1996](#)) are more fundamental than the sex difference in parental investment emphasized by [Bateman \(1948\)](#) and [Trivers \(1972\)](#), but the essence of the theory is unchanged: male mammals have been subject to sexual selection favoring intrasexual competitive inclinations and abilities more than has been the case for females because (and to the degree that) a female must invest more time or energy than a male in order to reproduce, making access to females the crucial resource that limits a male's fitness.

The mate choice component of sexual selection sometimes acts in concert with same-sex competition, such as when females evaluate males on the basis of the size or symmetry of weapons, or when they actively select the winners. More often, however, female choice appears to favor somewhat different male design features than those that are useful for fighting (see, e.g., [Moore and Moore \(1999\)](#) and [Norry et al. \(1999\)](#)). Much research has been concerned with demonstrating that females respond to male attributes that are informative with respect to the male's genetic quality, especially his genotype's success in resisting locally prevalent strains of disease organisms. Some of these attributes, such as aerobic capacity, are selected for both by female choice and by their effects in male–male competition, but others, such as elaborate

display organs or pheromones, probably function only in mate choice and not in intrasexual competition. In addition, females often select mates on the basis of the resources that they offer (e.g., territories, nest sites, gifts of food, and status) and although these various sorts of wealth are not necessarily traits that impart success in male–male competition, they are things that males compete to attain or monopolize. The effect is that mate choice by females selectively reinforces male abilities and inclinations to compete with one another, whether females attend directly to male performance in competitive confrontations or not.

What is responsible for variations in the intensity of intrasexual competition? A major factor is certainly the extent of male polygamy. Where male fitness variance is relatively large, the prize to the winners of aggressive competitions is also large, and there are large numbers of losers who are denied mating access; both these considerations favor the use of relatively extreme, reckless tactics. This principle is especially clear in comparisons across groups of related species such as seals or ungulates: the more polygamous the species (as indicated by the variance in male reproductive success or the numbers of females in the harems of the most successful males), the larger the sex differences in body size, weaponry, and violent combat, as well as in other forms of risk taking and in mortality schedules (see, e.g., [Daly and Wilson \(1983\)](#)). However, the same principle applies to variations within species, too. Unmated males have less to lose than those who already have a mate, for if the latter are contributing to the prospects of their progeny, or even just guarding the mates that they have acquired, then they are likely to evaluate the prospective costs and benefits of overt competition over access to a new female somewhat differently than unmated males, and are likely to be less reckless in the pursuit of new mating opportunities. In the human case, these considerations suggest that we should see not just sex differences in intrasexual competition, but differences in relation to the actors' marital and parental statuses as well, and we might also expect to see patterned variation as a function of life stage, cues of the intensity of local competition, and cues indicative of one's life prospects.

### 89.2.4 Homicide as an Assay of Competitive Confrontation and Risk Taking

How is the notion that intrasexual competition is a predictable consequence of sexual selection relevant to interpersonal violence? Homicide refers to lethal

violence undertaken privately (i.e., excluding killing that is socially legitimized, such as in war). It can be looked on as a form of risk taking since many cases culminate confrontational conflicts in which both parties risked injury, death, or arrest, and even when killers do not put themselves in physical danger they risk dire legal consequences. Most homicides involve a victim and a killer who are unrelated men, more often acquaintances than strangers, and most are transparently competitive, although the contested resources are not necessarily material ones. The competitive element in robbery homicide is obvious: one party had something that the other wished to usurp. Also clearly competitive are jealous killings of sexual rivals, although the contested resource is now a person. These two conflict typologies are both extremely common, but there is a third variety that is even more prevalent, especially where homicide rates are relatively high, such as is the case in many US cities: disputes over intangible social resources like face and respect ([Daly and Wilson, 1988](#)). In the criminological literature, these escalated status disputes and insult-precipitated killings are called trivial altercations, but in their social context, these disputes are not trivial. The precipitating insult may seem petty, but it is usually a deliberate provocation (or is perceived to be), and hence a public challenge that cannot be shrugged off. It often takes the form of disparaging the challenged party's manhood: his nerve, strength, or savvy, or the virtue of his wife, girlfriend, or female relatives. If there is a disparity in social rank, the high-status man may be able to ignore a challenge without loss of face, but not when the two are approximate equals. The challenge itself is likely to have been issued in response to status-inappropriate behavior: offense was taken because one party was elevating himself by putting on superior airs or failing to show deference to those of slightly higher rank. In these regards, homicidal altercations among low-status men resemble killings in defense of personal honor that are celebrated as heroic in other social contexts, especially when the killer is of higher status.

One interesting question is why these contests must continue to a deadly end. Sometimes, there seems to be almost an agreement that the conflict will be resolved violently (see, e.g., [Luckenbill \(1977\)](#) and [Toch \(1969\)](#)), and it is often the eventual victim who forces the issue ([Wolfgang, 1958](#)). The eventual killer may announce and justify his deadly intentions both to his victims and to their audience. In these features, the homicidal altercation seems more like a

formal duel (see, e.g., [Baldick \(1965\)](#) and [Williams \(1980\)](#)) than a senseless eruption of violence. The vigilant maintenance of a reputation for refusing to tolerate insult or disrespect is likely to have a deterrent effect on the probability of further disrespect, trespass or abuse, and such deterrence is particularly important when one cannot rely on dispassionate third parties such as the law to protect one's interests ([Nisbett and Cohen, 1996](#)). In a sociable species such as our own, where success and failure in competition have lasting social consequences mediated by rank and reputation, we expect an evolved inclination to display one's competitive risk-taking skills, and this should be especially characteristic of males ([Wilson and Daly, 1985](#)).

As would be expected from the combined considerations that most homicides entail competition between unrelated same-sex rivals and that intrasexual competition during human evolution was more intense in males than in females, the victims and killers in these competitive conflicts are overwhelmingly male. It is perhaps especially noteworthy that this is true even of the victims of robbery homicides, despite the fact that women are as likely as men to be victims of nonlethal robbery ([Wilson and Daly, 1985](#)). There may be several reasons for this, but at least part of the explanation seems to lie in the fact that robbery homicides often contain the same elements of competition and face that characterize altercations. This point is nicely made by [Toch \(1969\)](#) who has analyzed violent escalation in police–suspect interactions in terms of the stubborn aggressiveness of both parties when concerned to maintain face in front of witnesses.

Of course, most altercations do not end in death, and most robberies do not either. We use homicides as our assay of the intensity of intrasexual competition, despite their relative rarity and possible atypicality, because killing is recorded more reliably and with less bias than any lesser manifestation of interpersonal conflict. If readiness to participate in dangerous competition varies in relation to a demographic or circumstantial factor, then so should the rates of these homicides, regardless of whether killing is (or formerly was) adaptive in such contexts or is instead a by-product of aggressive motives that evolved to produce nonlethal effects. [Buss \(1999, 2000\)](#) has argued that the prevalence of homicidal fantasies, and the fact that many killings are intentional (rather than being accidents or slips), are reasons to doubt that homicide is a nonadaptive by-product of psychological adaptations and to

conclude that what we are studying is the behavioral outputs of psychological adaptations for homicide. This argument is unpersuasive (at least to us) because neither fantasy nor intent is a criterion by which one can distinguish adaptations from by-products. People intend to watch their favorite TV shows or feed their cats more often than they intend to kill, for example, but that does not imply that these actions are adaptations in their own right rather than being by-products of adaptations. Similarly, whereas many male undergraduates indeed report that they have had homicidal fantasies, even higher proportions of the men in one study reported that they had fantasized that they were flying, that they were playing video games, and that they had won the lottery; obviously, human beings possess psychological adaptations for none of these things ([Kai, unpublished BSc thesis](#)). In any event, epidemiological analyses of homicide can be used to test evolutionary psychological hypotheses, as illustrated later, regardless of whether there are aspects of the human psyche that deserve to be considered adaptations for lethal action, and regardless of whether homicide typically promotes the killers' fitness or ever did so in human ancestry.

### 89.2.5 The Sex Difference in Human Intrasexual Competition and Violence

Both the intensity of social competition and the local homicide rate are hugely variable in time and space, but one difference is apparently universal: men kill unrelated men at vastly higher rates than women kill unrelated women, everywhere ([Table 1](#)).

Criminologists and other social scientists have offered a wide range of hypotheses to explain sex differences in the use of lethal violence. Many such theories attribute men's greater use of violence to local aspects of particular societies, and thus shed no light on the phenomenon's cross-cultural universality (see, e.g., [Daly and Wilson \(1988, pp. 149–157; 1990, pp. 86–87\)](#)). Others invoke the human male's greater size and strength, but although this might explain an asymmetry in the use of violence against the opposite sex, it can hardly be said to predict or account for the sex difference in [Table 1](#); one might as readily have predicted that the group with the physical capacity to inflict the most damage (i.e., men) would be attacked least. The crucial omission from most such discussions of gendered behavior in the social sciences is of course some consideration of the effects of our sexual selective history. In any species in which the zero-sum game that partitions

**Table 1** Numbers of same-sex nonrelative homicides in various studies for which information on sex and relationship of killer and victim were available<sup>a</sup>

	<i>Homicides</i>	
	<i>Male</i>	<i>Female</i>
Chicago 1965–89	9761	229
Detroit 1972	316	11
Miami 1980	358	0
Canada 1974–90	3881	94
England and Wales 1977–90	3087	108
Scotland 1953–74	143	5
Iceland 1946–70	10	0
Tzeltal (Mexico) 1938–65	15	0
Bison-Horn Maria (India) 1920–41	36	1 <sup>b</sup>
Munda (India)	34	0
Oraon (India)	26	0
Bhil (India) 1971–75	50	1 <sup>b</sup>
Tiv (Nigeria) 1931–49	74	1
BaSoga (Uganda) 1936–55	38	0
Gisu (Uganda) 1948–54	44	2
Banyoro (Uganda) 1936–55	9	1 <sup>b</sup>
Alur (Uganda) 1945–54	33	1 <sup>b</sup>
BaLuyia (Kenya) 1949–54	65	3 <sup>b</sup>
JoLuo (Kenya) c. 79	22	2 <sup>b</sup>
IKung San (Botswana) 1920–55	12	0

<sup>a</sup>Data from [Daly M and Wilson M \(1988\) \*Homicide\*](#). New York: de Gruyter, and unpublished data.

<sup>b</sup>Victim and killer were unrelated co-wives of a polygynous man in the lone female–female cases in the Maria, Bhil, Banyoro, and Alur samples, as well as in one of the three BaLuyia cases and one of two JoLuo cases. We include co-wife cases, despite otherwise excluding marital as well as genetic relatives, because unrelated co-wives represent a female analogue of male–male rivalries.

ancestry among males is played with different rules or parameters than the corresponding game among females, the selective process will favor different attributes, including psychological attributes, in the two sexes. Any attempt to explain the phenomena in [Table 1](#) that presupposes the psychological identity of the sexes is a nonstarter.

Sex-differential violence against same-sex antagonists appears to be one of many manifestations of the fact that the human male psyche has evolved to be more risk accepting in competitive situations than the female psyche ([Wilson and Daly, 1985; Daly and Wilson, 1990, 1993](#)). Our sex difference in competitive violence is not unique: other species in which the variance in fitness (and the risk of total reproductive failure) is greater for males than for females exhibit the same thing. The evidence that human beings evolved under chronic circumstances of a somewhat greater fitness variance among males than among females is abundant and consistent. Even in societies

where people live by hunting and foraging, with much less disparity of wealth than is seen in agricultural societies or modern states, some men monopolize several women and thereby consign others to bachelorhood, with the result that variance in offspring production is greater among men than among women ([Howell, 1979; Hewlett, 1988; Hill and Hurtado, 1995](#)).

As noted earlier, the natural selective link between such a mating system and sex differences in competitive violence is well understood: basically, greater fitness variance selects for greater acceptance of risk in the pursuit of scarce means to the end of fitness (e.g., [Daly and Wilson, 1988](#), pp. 163–168). Furthermore, reckless life-threatening risk proneness is especially likely to evolve where staying alive by opting out of competition promises to yield no fitness at all and is therefore the natural selective equivalent of death ([Daly and Wilson, 1988; Rubin and Paul, 1979](#)). It is not surprising to an evolutionist that men compete with one another more intensely and dangerously than do women, and that this sex difference apparently transcends cultural diversity.

### 89.2.6 Demography of Masculine Competitive and Risk-Taking Inclinations

For further insight about sources of variability in violence, beyond the ubiquitous sex difference, the best models are likely to be those that incorporate sources of variance in social competition and the likelihood of reproductive failure in ancestral environments, and propose cues by which actors detect and respond to these variations. We propose that dangerous competitive violence reflects the activation of a risk-prone mindset that is modulated by present and past cues of one's social and material success, and by some sort of mental model of the current local utility of competitive success both in general and in view of one's personal situation. Thus, sources of variability in addition to sex might include the potentially violent individual's age, material and social status, marital status, and parental status; local population parameters such as the sex ratio, prevalence of polygamy, and cohort sizes; and ecological factors that affect resource flow stability and expected life span. Only a few of these factors have been extensively studied with respect to their possible impacts on violence, and some have scarcely yet been considered at all.

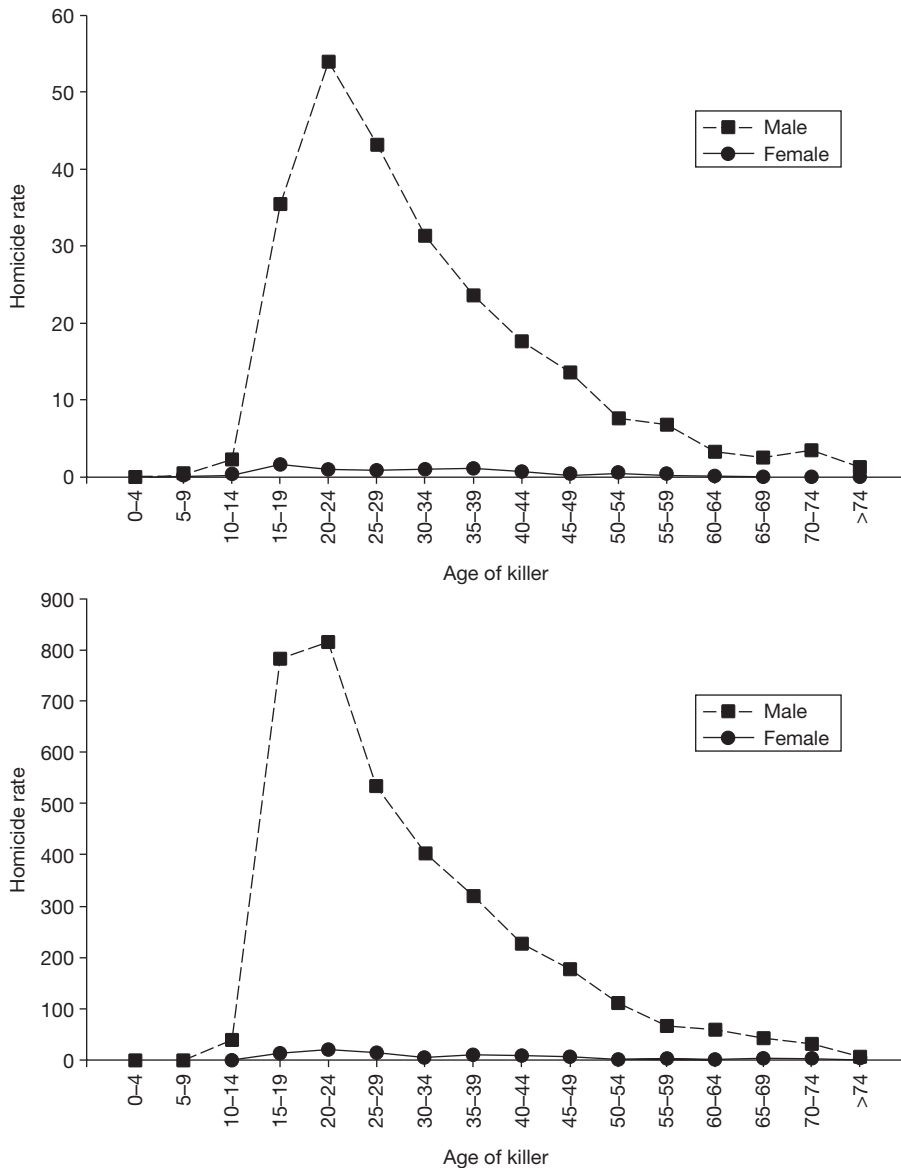
Criminal violence exhibits an age pattern that is almost as dramatic and consistent as the sex



difference: Offending rises rapidly after puberty, reaches a peak in young adulthood, and then slowly declines. **Figure 1** illustrates this pattern with homicide data.

This pattern is characteristic of other violent crimes such as robbery and sexual assault (see, e.g., [Thornhill and Thornhill \(1983\)](#) and [Chilton \(1987\)](#)), and of noncriminal confrontational risk taking as well ([Hilton et al., 2000](#); [Moffitt, 1993](#)). Challenging

criminologists, [Hirschi and Gottfredson \(1983, p. 55\)](#), to explain this striking pattern asserted that “the age distribution of crime is invariant across social and cultural conditions,” and that it “cannot be accounted for by any variable or combination of variables currently available to criminology.” Expanding on these assertions, [Hirschi and Gottfredson \(1986\)](#) argued that changes in employment status cannot explain why offending decreases with age,

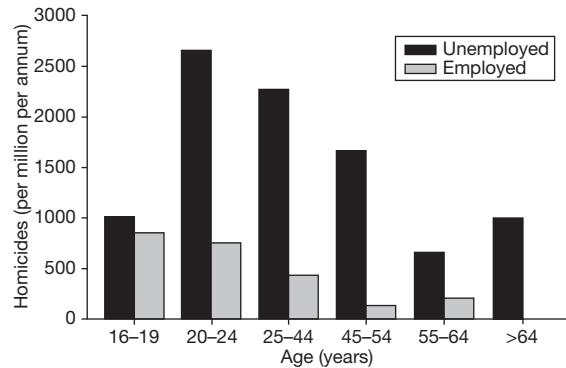


**Figure 1** Age-specific homicide rates (homicides per million persons per annum) for men and women who killed an unrelated person of the same sex in Canada, 1974–92 (upper panel), and in Chicago, 1965–89 (lower panel). Data include all homicides known to police in which a killer was identified. Data from [Wilson M and Daly M \(1994\)](#) A lifespan perspective on homicidal violence: The young male syndrome. In Block CR and Block RL (eds.) *Proceedings of the 2nd Annual Workshop of the Homicide Research Working Group*, pp. 29–38. Washington, DC: National Institute of Justice.

citing evidence that working and nonworking teenagers incur similar arrest rates; that an age-related decline in the proportion of men who are unmated is likewise irrelevant, citing evidence that delinquent boys are more, not less, likely to have girlfriends than their nondelinquent age-mates; and that becoming a father plays no role either, although on this point they cited no evidence at all. Thus, they maintained, “Change in crime with age apparently cannot be explained... by change in the social situation of people over the course of life” (Hirschi and Gottfredson, 1986: 67), and social explanations having failed, these sociologists concluded that the age-crime curve must be a reflection of human biology.

The assumptions that a biological explanation is an alternative to a social one and that its domain of applicability is that which is invariant are of course quite at odds with the evolutionary perspective outlined earlier. If it were true that a man’s likelihood of doing violence were unaffected by his material and social circumstances, this would be as surprising to an evolutionary biologist or psychologist as to a sociologist, since natural and sexual selection is expected to shape the psychology underlying risky competition in such a way as to modulate behavior in relation to one’s circumstance. A married father has more to lose in an altercation than a childless bachelor of the same age, for example, and it is implausible that the human psyche should have evolved to ignore such factors. To say this is not to deny that there is an evolved human life course, such that young men are specialized, both physically and psychologically, for competitive risk acceptance; male muscle strength and aerobic capacity, for example, rise and fall in a pattern rather like that of the age-crime curve, even when effects of exercise are controlled, and various sorts of voluntary risk-taking rise and fall similarly (Daly and Wilson, 1990). What is scarcely plausible is that either competitive inclinations or the evaluation of risks should have evolved to follow a life span trajectory that is impervious to one’s personal circumstances and associated cues of risk’s costs and benefits.

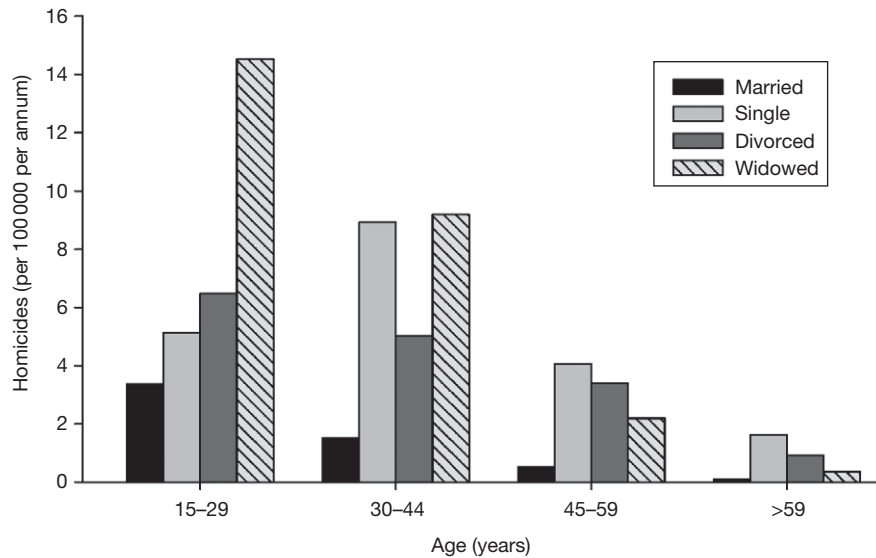
So is Hirschi and Gottfredson’s (1986) conclusion that social circumstance is irrelevant to the age-crime curve correct? Certainly not with respect to homicide: although employment status (Figure 2) and marital status (Figure 3) are poor predictors of offense rates by teenagers, they are very good predictors at subsequent ages, with the employed and the married much less likely than other men to become involved in the sorts of lethal disputes that we



**Figure 2** Age-specific homicide rates (homicides per million men per annum) for men who have killed an unrelated man, according to whether the killer was employed or unemployed for Detroit 1972. Data from Wilson M and Daly M (1985) *Competitiveness, risk-taking and violence: The young male syndrome. Ethology and Sociobiology* 6: 59–73.

interpret as competitive (Wilson and Daly, 1985; Daly and Wilson, 1990). A complication is that single men may differ from their married counterparts with respect to attributes that have causal impact on both their single status and their violence, but the notion that marriage is itself pacifying, and not simply a correlate of more relevant unmeasured variables, gains support from the observation that both divorced and widowed men apparently behave more like never-married men of the same age than like married ones (Figure 3). One could argue that the divorced are another selected subset who are more violent by disposition than those who stay married, but this sort of selection argument seems less plausible for the widowed. These data are also reminiscent of the longitudinal study by Mazur and Booth (1998), which indicated that T levels are reduced in married men, compared to same-age single men in the same profession (the US military), and that they rise again in those who divorce. We tentatively conclude that marriage’s apparent pacifying effect on men really is an effect.

It should of course be noted that we have not explained away the age-crime curve by these analyses. Although employment status and marital status make a big difference, massive age effects persist in Figures 2 and 3. Whether fatherhood has pacifying effects over and above those of marriage we cannot say, as no substantial homicide data set contains the requisite information, and, of course, no one has yet assessed the simultaneous impacts of these several factors. Thus, exactly how much of the age-related variability in crime will eventually be attributed to



**Figure 3** Age-specific homicide rates (homicides per million men per annum) for men killing unrelated men, according to the killer's marital status in Canada, 1974–90. Data from [Daly M and Wilson M \(2001\)](#) Risk-taking, intrasexual competition, and homicide. In: French JA, Kamil AC, and Leger DW (eds.) *Nebraska Symposium on Motivation, Vol. 47: Evolutionary Psychology and Motivation*, pp. 1–36. Lincoln, NE: University of Nebraska Press.

age-related changes in social and material circumstances, and whether an age–crime curve will persist when all correlated social factors are controlled is still unknown.

### 89.2.7 Discounting the Future

The rate at which one discounts the future is the rate at which the subjective value of future consumption diminishes relative to the alternative of present consumption (or, if you like, the interest rate required to motivate foregoing consumption). If A discounts more steeply than B, then A values present rewards more highly relative to future rewards than B, and is less tolerant of delay of gratification.

Psychologists, economists, and criminologists have reported that young adults, the poor, and criminal offenders all tend to discount the future relatively steeply. [Wilson and Herrnstein \(1985\)](#), for example, reviewed persuasive evidence that men who engage in predatory violence and other risky criminal activity have different time horizons than law-abiding men, weighing the near future relatively heavily against the long term. There are many terms for such a tendency, most of them pejorative: impulsivity, myopia, impatience, lack of self-control, and inability to delay gratification. Behind the use of such terms lies an implicit, false presumption that there is a single

right answer to the adaptive problem of how one should value present rewards relative to more distal ones, independent of life stage and socioeconomic circumstance, and that steep discounting is therefore pathological. By contrast, an evolutionary perspective suggests that adjusting one's personal time horizons can be an adaptive response to predictive information about the stability of one's social order and ownership rights and one's expected longevity ([Daly and Wilson, 1990, 2005](#); [Rogers, 1994](#); [Sozou, 1998](#); [Daly and Wilson, 2005](#)) as well as being a facultative response to one's current situation and perceived opportunities ([Wilson and Daly, 2004](#); [Van den Bergh et al., 2008](#)).

Much of the literature on these matters equates impulsivity with low intelligence, a prejudicial view that is perhaps based on the premise that an ability to plan for a distant future is a hallmark of the cognitive skills that make humans unique. The trouble with this anthropocentric view is that the problem of how to discount the future confronts all creatures. Indeed, it is the same problem as that addressed by [Fisher \(1930\)](#) and by all subsequent life-history theorists: How should the future be weighted in deciding present allocations of effort (see, e.g., [Clinton and LeBoeuf \(1993\)](#), [Grand \(1999\)](#), and [Roitberg et al. \(1992\)](#))? The right answer depends on statistical expectations of the present and future reproductive

payoffs of alternatives, which vary in relation to cues to which organisms – brainless creatures (and plants) as well as sophisticated cognizers – have evolved facultative responses. By this reasoning, what selects for delay of gratification is a high likelihood that present somatic effort can be converted to future reproduction, and rather than reflecting stupidity, short time horizons are predictable attributes of those with short life expectancies, those whose likely sources of mortality are independent of their actions, and those for whom the expected fitness returns of present striving are positively accelerated rather than exhibiting diminishing marginal returns.

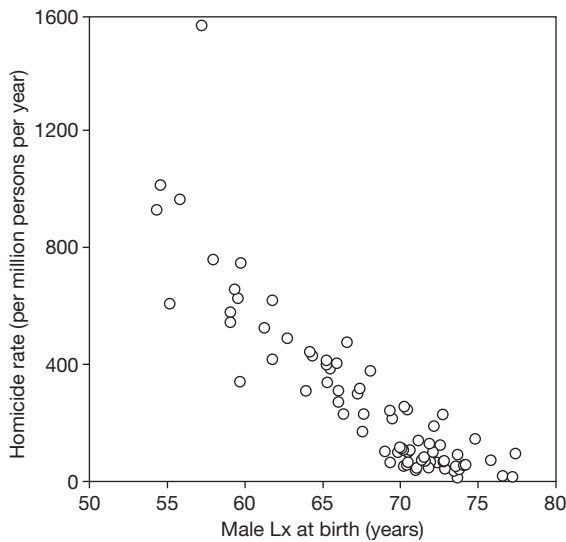
How human beings and other animals discount the future has been described in some detail by experimental psychologists, but a fuller understanding of these processes requires an infusion of evolutionary insights. The most noteworthy conundrum concerns the shape of discount functions, which are often, perhaps typically, hyperbolic (Kirby and Herrnstein, 1995). Hyperbolic discounting is puzzling because it engenders predictable reversals of preference between alternative futures as time passes, and hence predictable regret of what will become bad decisions in retrospect, with the result that people and other animals will even work to erect impediments to their own anticipated future choices of action (Kirby and Herrnstein, 1995). Why are the psychological underpinnings of time preference such as to produce these seemingly maladaptive internal struggles? This question can only be addressed by interpreting the relevant decision processes as adaptations to the structure of problems in nature, and Kacelnik (1997) has provided a satisfying answer to this particular problem, by showing that hyperbolic discounting is an expected consequence of mental evaluations whose function is to maximize rate of return while foraging or otherwise investing time in a task with sporadic returns. The experiments that produce hyperbolic discounting require animals to choose between rewards, after alternative delays that are unaffected by what one does during the delay and are followed by obligate time-outs which make the longer delay the optimal choice. The natural world contains no such problems. Instead, animals must choose among alternative activities with different expected rates of return (e.g., prey encounter rates), and the opportunity to resume foraging after an interval is typically under one's own control. Thus, with a psychology adapted to the problem of allocating efforts among endeavors with sporadic payoffs, evolved decision makers treat delays as time invested

in the task, and get it wrong only because of the artificiality of experimental situations.

Rogers (1994, 1997) has brought evolutionary reasoning to bear on the issue of optimal age-specific rates of future discounting, given the age-specific mortality and fertility schedules of human populations. His analysis suggests that people of both sexes should have evolved to have the shortest time horizons and to be maximally risk accepting in young adulthood. More specifically, his theoretical curve of age-specific optimal discount rates looks very much like the actual life span trajectory of reckless risk proneness that may be inferred from accidental death rates and homicide perpetration. This striking result seems paradoxical, given that we might expect indicators of a short or uncertain expected future life span to be responded to as cues favoring risk acceptance, but certain peculiarities of human life history and sociality, namely, gradually diminishing fertility long before death and a shifting allocation of familially controlled resources between personal reproductive efforts and descendants' reproductive efforts, dictate Rogers's counterintuitive result. One implication of this analysis is that a young adult peak in competitive risk taking may be a human peculiarity, while other species, including even our close relatives, the great apes, will exhibit monotonic increases in these tendencies into old age (Daly and Wilson, 2005). Comparative research on this question is needed.

As argued earlier, homicide and other criminal violence can be considered outcomes of steep future discounting and risky escalation of social competition. On the assumption that people are sensitive to social information predictive of their probable futures, Wilson and Daly (1997) hypothesized that homicide rates would vary as a function of local life expectancy, and tested this idea in Chicago, a city divided into 77 long-standing neighborhoods with relatively stable social and economic characteristics. In 1990, male life expectancy at birth in these neighborhoods ranged from 54.3 to 77.4 years, even with the effect of homicide as a cause of death removed, and this life expectancy proved to be the best available predictor of neighborhood-specific homicide rates (which ranged from 1.3 to 156 homicides per 100 000 persons per annum): the bivariate correlation between these variables was  $-0.88$  (Figure 4).

Might people actually be tracking something akin to local life expectancy? At present, we cannot disentangle possible effects of low or uncertain life span from the closely linked problems of low and



**Figure 4** Neighborhood-specific homicide rates (homicides per million persons per annum) in relation to male life expectancy at birth (with effects of homicide mortality removed) for 77 community areas of Chicago, 1988–93. Data from Wilson M and Daly M (1997) Life expectancy, economic inequality, homicide, and reproductive timing in Chicago neighbourhoods. *British Medical Journal* 314: 1271–1274.

uncertain future resource flow, and other evolution-minded social scientists have emphasized the latter sort of uncertainty as the factor favoring short time horizons (Hill et al., 1997). However, it is conceivable that the human psyche computes something functionally equivalent to an estimate of the distribution of local life spans, based on the fates of salient others; if several family members and friends have died young, discounting the future would follow. Moreover, if this mortality appeared to be due to bad luck that was independent of the decedents' behavior, it would be all the more adaptive to respond by accepting risks in the pursuit of short-term advantage. If such inference processes exist, they are unlikely to be transparent to introspection, but they may be revealed in attitudes and expectations, and it is interesting in this regard that testimony of the US urban poor contains many articulate statements about the specter of early death, the unpredictability of future resources, and the futility of long-term planning (see, e.g., Hagedorn (1988) and Jankowski (1992)). An interesting question for psychological research is how mental models and subjective parameters in these domains develop over the life span; another is whether media representations (including fictitious ones) affect these inference processes and their

development in the same way as real information about neighbors and relatives.

Local life expectancy appears to be predictive of future discounting in nonviolent domains, too, and we suggest that life expectancy cues may affect investments in the future through education, preventive health measures, and savings, as well as the timing of major transitions and life events. In Chicago, rates of truancy (school absenteeism for nonmedical reasons) are high where life expectancy is low, and somewhat surprisingly, this relationship is stronger for primary school truancy than for high school (Daly and Wilson, 2001); one interpretation is that parents' motivation to invest in education by enforcing school attendance varies in relation to cues of the chances that doing so will eventually pay off. Teenage pregnancy is another phenomenon in which perceptions of local life expectancy or life prospects may play a role: although early reproduction is widely deemed a social pathology, reflecting a failure to exercise choice, Burton (1990) and Geronimus (1992, 1996) report that poor teenage mothers are active decision makers who expressly wish to become mothers and grandmothers while still young and efficacious because they anticipate problems of early weathering, poor health, and a life course more compressed in time than that of more affluent people. Wilson and Daly (1997) interpret age-related fertility patterns in Chicago neighborhoods accordingly.

### 89.2.8 Inequity and Lethal Competitive Violence

Homicide rates are highly variable between times and places (see, e.g., Archer and Gartner (1984) and Eisner (2003)), and the discussion earlier suggests that much of this variance may be attributable to variance in the severity of male–male competition. When rewards are inequitably distributed and those at the bottom feel they have little to lose, escalated tactics of social competition, including violent tactics, become attractive. When the prize for competitive ascendancy is smaller, and even those at the bottom have something to lose, such tactics lose their appeal. One might therefore expect that income inequality will account for a large share of the variance in homicide rates.

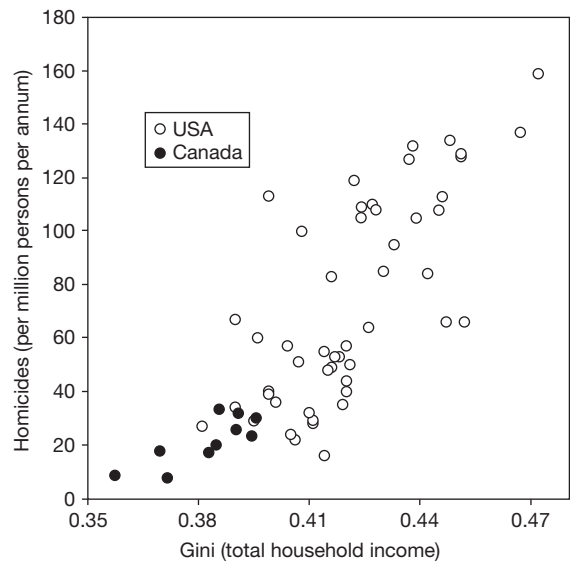
This expectation is upheld. In cross-national analyses, the Gini index of income inequality (which ranges from 0 at perfect equity to 1 when all income accrues to the single wealthiest unit) consistently outperforms most other predictors of homicide

rates, including various indices of average income or welfare, suggesting that it is relative rather than absolute deprivation that has the greater effect on levels of violent competition (Daly et al., 2001). Only the Gartner (1990) study disaggregated the overall homicide rate, and she found that income inequality predicts the rates at which adults, but not children, are killed, and is a stronger predictor of men's than of women's victimization. In general, the results of these cross-national studies are highly compatible with the proposition that homicide rates assay the local intensity of competitive conflict, especially among men.

Research on income inequality and homicide rates within, rather than between, nations is relatively scarce, but the results have been striking. Kennedy et al. (1996) found that the Gini index was significantly correlated with many components of mortality across the 50 US states in 1990, but with none more highly than homicide ( $r = 0.73$ ). Blau and Blau (1982) found that income inequality accounted for more of the variance in homicide rates among 125 US cities than other measures including percent below the poverty line. At a still finer level, namely across the 77 Chicago neighborhoods, the correlation between the Gini index and the homicide rate is even higher ( $r = 0.81$ ; Daly et al., 2001).

Despite this abundant evidence, the proposition that inequity *per se* is relevant has remained somewhat controversial because high income inequality is generally associated with a low level of economic development and average welfare, and even though the Gini index usually predicts the homicide rate better than other economic indicators, one might still argue that it is somehow just a better indicator of general prosperity. Analyses of Canadian homicide data (Daly et al., 2001) refute this hypothesis: the most inequitable Canadian provinces are the richest ones, in direct contrast to the correlations across US states and Chicago neighborhoods, but the positive association between the Gini index and homicide is undiminished ( $r = 0.85$ ). Moreover, the data for the Canadian provinces and the United States lie almost exactly on the same regression line (Figure 5). These results suggest that the single variable of economic inequality is largely responsible for the notorious difference in these neighboring countries' homicide rates.

The dramatic association between inequitable access to resources and homicide in modern nation-states may not extend to traditional nonstate societies like those in which we evolved. Homicide rates in modern hunter-gatherer societies generally dwarf those of modern nation-states (Daly and Wilson, 1988),



**Figure 5** Homicide rates (homicides per million persons per annum) in relation to the Gini coefficient (based on total household income) for the 50 United States, 1990, and the ten provinces of Canada, 1988–92. Data from Daly M, Wilson M, and Vasdev S (2001) Income inequality and homicide rates in Canada and the United States. *Canadian Journal of Criminology* 43: 219–236.

even though economic (material) inequity is seldom extreme. One reason for high homicide rates in these relatively egalitarian societies is the absence of modern medicine, which makes a broader range of wounds life-threatening, but a possibly more important reason is the absence of police power and an effective system of disinterested third-party justice: without effective police and judiciary, a credible threat of personal or kin violence is a crucial social asset regardless of one's wealth or status, and as noted earlier, the familiar tendency for violence to be primarily a recourse of the disadvantaged disappears. Moreover, although an inequitable distribution of wealth is less conspicuous in face-to-face societies than in modern nation-states, inequitable access to marital and reproductive opportunities may actually be more extreme and highly salient. In any case, we would still expect that *ceteris paribus*, dangerous tactics of social competition, will be more attractive to those who have less to lose.

Our Chicago analyses, plus consideration of the social environments in which humans evolved, make us suspect that the social comparison processes mediating the effects of inequity probably operate at more local levels than considered in most criminological and economic research on income inequality's

effects. The lives and deaths of personally known individuals are especially salient to one's mental model of one's life prospects. Nevertheless, it is also interesting to ask whether a more global perception that one lives in a winner-take-all society (Frank and Cook, 1995) inspires competitive escalation, and whether media portrayals (including even fictional ones) affect mental models of the rewards available to the winners.

Social scientists have long been interested in the socially undesirable effects of inequality. What an evolutionary psychological approach adds is the suggestion that inequality has its effects not simply by virtue of nonadaptive stress effects, but also by inspiring a rational escalation of costly tactics of social competition. This consideration complicates causal analysis, because it implies that the distribution of age-specific mortality is more than an outcome variable, having feedback effects on its own causal factors and hence on itself. Although we excluded homicide mortality from our analyses of the apparent effects of life expectancy, for example, in order to eliminate spurious autocorrelational effects, it is likely that local levels of homicidal violence affect expectations of future life, discount rates, and hence further violence. Inequality is also expected to affect expectations of future life and discount rates.

### 89.2.9 Making Sense of Individual Differences

We have stressed that theory and research in psychology, including evolutionary psychology, has been more concerned with characterizing panhuman nature than with human diversity. But diversity exists, and it too requires evolutionary explanation. Much behavioral heterogeneity depends, of course, on the contingent responsiveness of the adult psyche to differences in circumstance, but not all can be explained as resulting from a shared set of if-then rules in conjunction with individual differences in one's current situation. Some, instead, derives from enduring personality traits established early in development. In explaining and predicting others' behavior, people attribute traits such as a short temper or jealousy or fair-mindedness to particular acquaintances because such attributions appear to carry useful information about the reasons for past actions and the likelihoods of future actions. This appearance is no illusion, for although attributions can be excessive or misguided, they do improve prediction. That is, stable

differences in personality do indeed account statistically for some substantial fraction of behavioral diversity (Kenrick and Funder, 1988).

Why this should be so is a conundrum from an evolutionary perspective. If selection favors an optimal species-typical design, it is challenging to address the question of individual differences in personality from an adaptationist perspective (Buss, 1991; Tooby and Cosmides, 1990). Why, for example, does violent aggressivity seem to be a personality variable? Why, in other words, should selection not have favored the optimal set of social psychological propensities (i.e., those that best promoted fitness in ancestral environments), with the result that everyone's behavioral repertoire would include more or less identical responses, including violent responses, to particular threats and challenges?

One plausible answer is that people are more alike in this regard than they appear, because human facultative responsiveness is largely developmental rather than just being a matter of contingent reaction to immediately present challenges. Consistent with this idea is the fact that experience with violence predicts its subsequent use (see, e.g., Coie et al. (1991) and Dodge et al. (1990a,b,c)); one reason why people are developmentally labile in this way could be that expertise in the use of violence raises its effectiveness and hence its appeal. Moreover, the information that is of relevance to adaptive decision making in dangerous confrontations has greater time depth than just the immediate situation: how short one's temper ought, ideally, to be, for example, depends on statistical attributes of one's social milieu that can only be induced (if at all) from cumulative experience over a long time.

There is substantial evidence that readiness to use violence is indeed developmentally labile, and some of this evidence suggests that this plasticity may be functional for the actors in the manner just suggested. In a cross-cultural analysis of child-rearing practices in nonstate societies, Low (1989) showed that in societies which have repeatedly engaged in war in recent history, parents and others strive to inculcate aggressivity, strength, skilled use of weapons, and tolerance of pain in boys more than is the case in nonwarring societies. Within Western industrialized nations, there is evidence that people with childhood experience of violence, whether as victims or as witnesses, are relatively likely to use violence (Dodge et al., 1990b; Widom, 1989). Longitudinal studies of juvenile delinquents and career criminals reveal a prior history of various social transgressions

including violence (see, e.g., [Wilson and Herrnstein \(1985\)](#), [Farrington \(1991\)](#), [Tonry et al. \(1991\)](#), and [Sampson and Laub \(1993\)](#)).

Psychiatrists have identified a personality type that is particularly likely to engage in violent aggressivity: the antisocial personality ([American Psychiatric Association, 1994](#)), which is often diagnosed in both juvenile offenders and career criminals ([Moffitt, 1993](#); [Olweus et al., 1986](#)). The diagnostic criteria for antisocial personality include a history of conduct disorder prior to age 15 and a continued pattern of disregard for and violation of the rights of others into adulthood ([American Psychiatric Association, 1994](#), p. 649). There are apparently a number of reliable risk factors associated with the development and maintenance of antisocial personality, including poverty, maleness, early maturity, poor school performance, parental criminal history and psychopathology, and having a lone mother in *loco parentis* (see, e.g., [Tonry et al. \(1991\)](#) and [Moffitt \(1993\)](#)). These risk factors largely overlap the risk factors for juvenile delinquency and violent crime (see, e.g., [Wilson and Herrnstein \(1985\)](#), [Farrington \(1991\)](#), and [Sampson and Laub \(1993\)](#)); moreover, the same risk factors characterize many urban communities with high rates of violence (see, e.g., [Krahn et al. \(1986\)](#), [Sampson \(1991\)](#), and [Coulton et al. \(1995\)](#)). All these considerations suggest that this so-called disorder is largely a reflection of a facultative developmental response to indicators of the futility of developing a more prosocial personality.

Notwithstanding these reasons for invoking facultative development, however, there is also considerable evidence from twin and adoption studies that antisocial personality is substantially heritable ([Carey, 1994](#); [Carey and Gottesman, 1996](#); [Lyons, 1996](#)). Thus, the question remains: Why does genetic variability affecting traits like antisocial personality persist? Behavior geneticists seldom consider their findings in the context of Darwinian selection, so the question has scarcely been addressed (but see [Rowe \(1994\)](#)). The available answers appear to be few. One possibility is that selection was weak in ancestral generations, so the variability was effectively neutral with respect to fitness. This is especially plausible when the attributes in question develop in interaction between the effects of particular genotypes and particular novel aspects of modern environments; sensitivity to novel chemical pollutants, for example, can be highly heritable, but these differential effects of the relevant genotypes were of no selective relevance in ancestral environments in

which those chemicals did not exist. Another possibility is that selection pressures have been heterogeneous in time and/or space, so that no single optimal phenotype could become universal across the population's whole range of environments ([Williams, 1992](#)). Finally, perhaps the most interesting possibility in the present context is that of frequency-dependent selection.

Alternative types are said to incur frequency-dependent selection when their respective fitnesses change as a function of their relative frequency (see, e.g., [Heino et al. \(1998\)](#)). In some animals, for example, there is a rare male mating advantage ([Ehrman, 1972](#)) such that whichever of two alternative types of male is rarer in a local population begins to be preferred by females, with the result that the rarer type outreproduces the commoner and neither is likely to go extinct. [Mealey \(1995\)](#) and accompanying commentaries discuss the possibility that sociopaths or psychopaths – an exploitative and often charming personality type apparently lacking empathy – might be maintained analogously in human populations, with their success as deceivers tending to be inversely correlated with their prevalence.

On this argument, psychopathology is not really a pathology at all, and we should not expect to see the signs of dysfunction that characterize unequivocally pathological states like autism, schizophrenia, or Down's syndrome. It is true that psychopaths are different from normal prosocial people in that they lack empathy, tolerate aversive stimuli, are more likely to use violence and coercion, and generally process emotional information differently ([Harris et al., 2001](#); [Quinsey et al., 1998](#); [Williamson et al., 1991](#); [Hare, 1996](#)), but are they defective, or just different, albeit in an unpleasant way? [Lalumière and Quinsey \(1996\)](#); [Quinsey et al. \(1998\)](#), [Lalumière et al. \(1999, 2001\)](#), and [Harris et al. \(2001\)](#) argue that the specific attributes that characterize psychopaths are intelligible design features of a frequency-dependent alternative reproductive strategy that cheats by exploiting the prosocial inclinations of the majority. One indication that psychopaths may not be defective is that they do not show the other signs of developmental damage that often accompany other serious psychiatric disorders; they differ from groups with other clinical diagnoses, for example, in the fact that they are no more likely than normals to have been the victims of complications at their births ([Harris et al., 2001](#)), and in the fact that their bodies are just as bilaterally symmetrical as those of normals ([Lalumière et al., 2001](#)).



### 89.2.10 Testosterone and the Modulation of Confrontational Competitive Risk Taking

There has been considerable controversy about the links between circulating levels of plasma T and behavior. However, the largest published study of the issue indicates that high T levels are associated with a variety of antisocial behaviors: among 4462 US military veterans, criterion groups who reported antisocial acts such as childhood truancy, violent behavior, military AWOL, drug and alcohol abuse, on-the-job problems, and marital disruption each had on average higher T-levels than those who did not report the acts (Dabbs and Morris, 1990; Booth et al., 1985; Booth and Osgood, 1993; Booth and Dabbs, 1993; Mazur, 1998). Dabbs et al. (1987, 1995) have also reported that T levels in a sample of incarcerated men were related to the violence of the crime. An earlier study (Ehrenkranz et al., 1974) had shown that chronically aggressive men in prison for violent crimes had higher levels of plasma T than nonaggressive men in prison for nonviolent crimes. Other researchers, however, have found no significant differences in T between men charged with murder or assault and those charged with property crimes (Bain et al., 1987). Descriptions of the behavior and attitudes of the incarcerated men in Dabbs's studies suggest that it is not the type of crime *per se* that is associated with elevated T-levels, but whether it entailed aggressive confrontation; the men with higher T were also characterized as tough by their peers (Dabbs et al., 1987) and were known for violating prison rules, especially rules involving overt confrontation (Dabbs et al., 1995).

There are some inconsistencies in the literature on associations between circulating T levels and individual differences in confrontational and competitive behaviors. However, according to Archer (2006), these may be explicable in light of the challenge hypothesis – a conceptual framework proposed by Wingfield (1984) and Wingfield et al. (1990) for understanding how androgen levels in vertebrates are modulated by aspects of the social environment. Wingfield et al. (1990) noted that in various species, transitory elevations in male T levels can be induced by interactions with receptive females and male-male interactions that constitute challenges to a male's territorial or reproductive interests. They argued that the extent of such androgen responsiveness to social cues should vary systematically across species, and between individuals, according to factors such as mating system and degree of paternal

investment. Moreover, they suggested that variation in the display of aggressive or confrontational behavior is likely to be more closely associated with T responsiveness to social modulation rather than absolute or baseline levels of T. Not all predictions made by Wingfield et al. (1990) have received empirical support, but evidence for social modulation of androgens, consistent with many aspects of the challenge hypothesis, has accumulated for nonhuman species (Oliveira, 2004; Hirschenhauser and Oliveira, 2006) and for men (Archer, 2006).

There is some evidence that men's T levels do increase after brief interactions with women (Roney et al., 2003, 2007) and after watching sexually arousing films (Pirke et al., 1974; Hellhammer et al., 1985; Stoléru et al., 1993, 1999). Moreover, there are numerous demonstrations that circulating T levels in men can be affected by social cues associated with involvement in competitive events. T-levels rise in anticipation of athletic contests such as tennis and wrestling matches, for example, and rise still higher in the aftermath of a victory, whereas there is no further rise or even a drop after a loss (Mazur and Lamb, 1980; Booth et al., 1989; Elias, 1981; Campbell et al., 1997). T responses to competition are not limited to physically demanding activities, but have also been seen in chess matches (Mazur et al., 1992), in a reaction time contest (Gladue et al., 1989), and even in games of chance with no element of skill (McCaul et al., 1992). The juice of victory may even be felt among spectators: Bernhardt et al. (1998) measured T-levels in fans watching the 1994 World Cup final on television, and found that supporters of the winning Brazilian side exhibited a postmatch increase while supporters of the losing Italian side exhibited a decrease. Even cichlid fish have been shown to experience vicarious endocrine responses, exhibiting increases in T levels after watching a dominance fight between conspecific males (Oliveira et al., 2001).

Not all studies find effects of competitive outcomes on T-levels, but even the exceptions may reflect interpretable variations in the meaningfulness of victory. There is some evidence that T increases in response to success in competitive encounters depend on a man experiencing mood elevation as a consequence of winning (McCaul et al., 1992) and the degree of mood elevation may depend on the salience of the competitive encounter for the individual. Gonzalez-Bono et al. (1999), for example, found no significant change in the average T-levels of winners or losers in a close professional basketball game, but

they did find effects in the players who purportedly played the largest role. Similarly, [Edwards et al. \(2005\)](#) found that the percent increase in T seen after having won a soccer match was positively associated with self- and other-rated connectedness with teammates. Other competitions may be unarousing because the outcome is a foregone conclusion: [Mazur et al. \(1992\)](#) found postmatch T-changes in chess winners and losers only when opponents were of similar ability.

Of course, T-responses, like average T-levels, may also exhibit individual differences, and one relevant attribute (perhaps intermediate in stability between a personality trait and a situational response) is the individual's inclination to compete and/or dominate. [Schultheiss et al. \(1999\)](#), for example, found that scores on a personal power motivation scale were positively correlated with T-responses to victory in a race to connect a series of numbers. Similarly, [Zumoff et al. \(1984\)](#) reported that men who are intensely competitive and impatient had higher daytime T-levels than more placid men. Moreover, there is evidence that T levels are generally high in men in action-oriented occupations like firefighters and paramedics ([Dabbs and Dabbs, 2000](#)).

The challenge hypothesis suggests that variation in the display of aggressive or confrontational behavior is likely to be more closely associated with T responsiveness to social influences rather than with absolute or baseline levels of T. Few studies, however, have investigated individual differences in T responsiveness in response to social challenges. However, the previously mentioned study by [Cohen et al. \(1996\)](#) found that among University of Michigan students (presumably a relatively nonviolent group), T-levels rose within 20 min after a verbal insult in men hailing from southern states, known for espousing the honor culture, but not in those from the North ([Cohen et al., 1996](#)). More recently, it has been shown that circulating T-levels after an experience of competitive success (which was actually experimentally determined) is highest in men with relatively masculine facial structure ([Pound et al., 2009](#)).

One adaptationist interpretation of the increase in T after a win is that the winners in social competition will soon be challenged again, and that increased T-levels help prepare tissues for such challenges ([Archer, 2006](#); [Wingfield, 1984](#); [Wingfield et al., 1990](#)). A related, and perhaps more general, idea is that victory and defeat are informative as regards one's likelihood of further success or failure in the near future, so that winners should continue to be assertive

both in male–male competition and in courtship, whereas losers are better advised to retrench and wait for better opportunities; the T-response may then be mediating the contingent modulation of sexual and aggressive motivation and initiative. Recent evidence suggests that, if experimentally allocated to a losing condition in a rigged competition, a man's T-response to the experience is predictive of the likelihood that he will choose to compete again ([Mehta and Josephs, 2006](#)).

It remains unclear through what proximate psychological mechanisms T might influence competitiveness and risk sensitivity. Recent evidence, however, suggests that acute administration of T (in women at least) can reduce attention to threatening stimuli ([Van Honk et al., 2005](#)), the magnitude of the fear-potentiated startle response ([Hermans et al., 2006a](#)), and empathetic behavior ([Hermans et al., 2006b](#)). Moreover, recent experimental evidence suggests that circulating T-levels are associated with cognitive processes that could have a proximate role in modulating confrontational and competitive behavior. [Burnham \(2007\)](#) measured T-levels in Harvard economics students playing the ultimatum game, a two-step procedure in which one party proposes a split of a windfall and the other then either accepts the offer, effectuating the proposed split, or rejects it, leaving both players with nothing. Men who rejected an anonymous peer's low and perhaps insulting offer of \$5 out of \$40 (the stingy condition) had higher T-levels, measured before playing the game, than those who accepted the offer. Unwillingness to accept outcomes that are perceived as unfair is likely to be related to a man's tendency to get involved in tit-for-tat disputes that could escalate into violent confrontations.

### 89.2.11 Testosterone as a Mediator of Mating Effort

Work in nonhuman species has indicated that testosterone may play a role in mediating life-history tradeoffs between reproductive and immune functions ([Muehlenbein and Bribiescas, 2005](#)) and that social modulation of T-levels may permit individual males to facultatively adjust their agonistic behavior according to their own competitive ability ([Oliveira, 2004](#)). Investigation of the links between T and behavior in humans has been complex and controversial not only because causal impacts are bidirectional, but also because there are simultaneous impacts on several analytically separable timescales.

At one extreme, stable personality differences must be invoked when interpreting findings such as the association between prison inmates' T-levels and the qualities of their past crimes (Dabbs et al., 1987, 1995). At the opposite extreme are the rapid T-responses to social experience reviewed earlier. Intermediate cases include perhaps the most important effects: changes in relatively chronic T-levels and behavioral practices over the life span and in relation to long-lasting social status attributes such as marriage and fatherhood.

As we might expect from the evidence that T is causally implicated in both sexual behavior and male–male competition, T-levels are low during most of prepubertal childhood (although there is a period of relatively high T-levels in infants, related to ongoing sexual differentiation), and they rise from puberty to a peak in young adulthood, then fall very slowly at about 1% per year (Liu et al., 2007), remaining above childhood levels into old age (Simon et al., 1992; Dai et al., 1981; Gray et al., 1991a,b; Field et al., 1994; Dabbs, 1990). This age pattern is reminiscent of the age–crime curve illustrated in Figure 1 and other age-related patterns of risk taking, although the peak in youth is less dramatic, and one is tempted to infer that these changes in T-levels play a role in mediating mating effort. This term (Low, 1978) refers to the allocation of one's time, energy, and attention to pursuits, including both courtship and male–male competition, that might pay off in mating opportunities, and is contrasted with the alternative form of reproductive effort, namely parental effort. Of course, correspondence between T levels and the age–crime curve cannot be taken to imply causation. As noted previously, involvement in social situations entailing competition and challenges to status can cause transient elevations in T-levels, and therefore plausibly could also have chronic effects.

In a predominantly monogamous species with biparental care, such as *Homo sapiens*, we might expect individuals who have acquired mates to reallocate time and energy from mating effort into other pursuits, and it is interesting in this context that T-levels have been shown to vary systematically in relation to relationship status. A number of studies have shown that, in North America, partnered men (i.e. married or in a committed relationship) have lower T (see, e.g., Gray et al. (2002), Burnham et al. (2003), Gray et al. (2002, 2004), and van Anders and Watson (2006)) and similar findings have now been reported in other populations. For example, among the Ariaal of Northern Kenya men with wives have significantly

lower T levels than unmarried men (Gray et al., 2007). A number of studies, however, have reported only marginal, nonsignificant, differences in T levels between partnered and unpartnered men (Gray et al., 2006; Sakaguchi et al., 2006, 2007).

In the large study of US military veterans mentioned earlier, not only was it the case that men with high T-levels were relatively likely to be single, or, if they did marry, to divorce (Booth and Dabbs, 1993), but there was also evidence that changing T-levels tracked marital status. The relevant data come from a 10-year longitudinal study of 2100 male US Air Force veterans (aged 32–68 years) whose T-levels were measured in 1982, 1985, 1987, and 1992: in a pattern reminiscent of the homicide data in Figure 3, the transition to marriage was associated with a fall in T-levels and divorce was associated with a resurgence (Mazur and Booth, 1998; Mazur and Michalek, 1998; but see Flinn et al. (1998)). A more recent (albeit much smaller) longitudinal study (van Anders and Watson, 2006), however, has suggested that differences in T levels between partnered and unpartnered men may arise as a consequence of stable individual differences in T levels that are systematically related to the likelihood of acquiring and maintaining partnered status (rather than being attributable to the effects of being partnered or not). If both elevated T-levels and homicide offending reflect the allocation of reproductive effort to mating effort, then it is not surprising that they exhibit parallel patterns associated with marital status, perhaps analogous to the seasonal changes in T-levels and mating competition that occur in some nonhuman species.

Recent reports indicate that married men's T-levels fall still further as parental effort is demanded: Gray et al. (2006) found that, in a sample of men from a Chinese university, fathers had lower T than both married men without children and unmarried men. Similarly, Storey et al. (2000) reported that T-levels in men were low around the time that their wives gave birth, especially in those fathers who scored high on indices of commitment to the pregnancy and the child. An obvious interpretation is that high T-levels interfere with paternal effort by inspiring greater allocation to mating effort instead, and are therefore adaptively reduced as part of getting into a paternally investing mode, an interpretation that is reinforced by parallel evidence in other biparental species, including some experimental evidence. In dark-eyed juncos, for example, Raouf et al. (1997) reported that males who were given T-implants reduced their levels of paternal care

relative to males with control implants, and were more likely than controls to sire offspring in rivals' nests, presumably because they put more effort into the pursuit of extrapair matings. Remarkably, these T-implanted male juncos were also less likely to be cuckolded themselves, presumably because they also defended their exclusive access to their own mates more effectively; little wonder that they had to cut back on feeding the nestlings!

In further support of the testosterone–mating effort connection in men, there is some intriguing evidence that individual differences in men's T-levels are predictive of their reported numbers of sexual partners (Dabbs and Dabbs, 2000; Booth et al., 1999; Kemper, 1990). However, what these studies might really reflect is a tendency for men with high T-levels to brag or exaggerate, and even if the effect is genuine, the direction of causality is not clear. Certainly, copulation can sometimes boost T-levels in nonhuman species such as male rats, for example (Hart, 1983). In humans, however, although evidence suggests that brief interactions with women (Roney et al., 2003, 2007) and sexual arousal associated with viewing erotic films (Pirke et al., 1974; Hellhammer et al., 1985; Stoléru et al., 1993, 1999) can both cause acute increases in T-levels, experimental evidence indicates that they are unaffected by sexual activity and orgasm (Exton et al., 2001; Krüger et al., 2003). There is evidence, however, that T levels may rise in anticipation of sexual activity. For example, nearly 40 years ago in an anonymous report in *Nature* (Anonymous, 1970), an author described how his beard growth (an androgen-dependent process) slowed during periods of isolation on a remote island but increased again in the days immediately prior to returning to the mainland and resuming sexual activity with his partner. More recent experimental evidence suggests that, relative to men who have not abstained, T-levels are elevated immediately prior to sexual arousal in men who have undergone a period of several weeks sexual abstinence (Exton et al., 2001). Consequently, it is possible to speculate that differences in T-levels between partnered and unpartnered men could be caused by differential exposure to periods of anticipatory abstinence.

### 89.2.12 Testosterone's Costs and Honest Signaling

A male's level of circulating T affects not only his own behavioral decision making, but the social signals that he emits and the reactions that he elicits

from others of both sexes. Female choice often favors males who maintain and somehow are able to display higher than average T-levels, although this may be less true of pair-forming biparental animal species than of species in which male fitness variance is high and paternal investment in young is nonexistent. Female meadow voles, for example, prefer intact high-T males over castrates on the basis of smell (Ferkin et al., 1997). In the black grouse, a bird in which females choose with whom to mate at a communal display ground and then nest alone without male help, T-levels (as well as seniority) predict which males will hold the advantageous central territories on the display ground and how many females will elect to copulate with them (Alatalo et al., 1996).

In red grouse, T-administration enhances the size (Mougeot et al., 2004) and redness (Mougeot et al., 2007) of the comb, but impairs T-cell-mediated immunity (Mougeot et al., 2004), and experimental reductions in nematode parasite load also increase comb redness (Martinez-Padilla et al., 2007). It has proven rather difficult to identify the phenotypic differences among displaying males by which female grouse choose males, but relevant cues have been discovered in many other bird species, with females showing sensitivity to detailed aspects of male secondary sexual traits or ornaments such as plumage brightness, long tails, and the size and coloration of featherless protruberances. (The evidence for fine female discriminations with respect to behavioral displays such as songs and aerobic maneuvers is much scarcer, but this should not be considered evidence of their lesser importance. They are just harder to measure and to manipulate experimentally than morphological ornaments.) That the more elaborately ornamented males indeed get a disproportionate share of paternity has now been documented with DNA evidence in a number of avian species (Møller and Ninni, 1998).

The dependence of male secondary sexual traits on androgens, both for their initial development and for their maintenance, is widely documented in a range of vertebrates (see, e.g., Pinxten et al. (2000), Wingfield et al. (1997), and Owens and Short (1995)). But why should females prefer males whose sexual ornaments are both androgen-dependent and brighter or otherwise more elaborate than average? One hypothesis that has been popular with theoretical biologists is that these traits and associated female preferences are arbitrary products of a runaway process whereby selection for the trait and for the preference reinforce one another until costs of

the trait stop the elaborative process. This model has never been as popular with field researchers, however, not just because it is hard to design a study that would demonstrate the process in nature, but because whenever preference criteria are carefully studied, they turn out not to be arbitrary, as the runaway model predicts, but to be carriers of useful information about the signaler. Accordingly, theories that posit that a female's mate choice criteria actually function to improve the quality of her offspring are in the ascendancy, and perhaps the most influential of these is that proposed by [Hamilton and Zuk \(1982\)](#).

Initially concerned only with birds, [Hamilton and Zuk \(1982\)](#) proposed that male display traits, especially plumage color and luster and the quality of songs, provide evidence of the male's current burden of disease microorganisms (pathogens), and of his past and present pathogen resistance (see also [Møller et al. \(1998\)](#)). One benefit of choosing a relatively pathogen-free male is reduced risk of disease transmission at the time of mating, but the function that Hamilton and Zuk stressed is more subtle: by mating with a male who is relatively resistant to whatever pathogen strains are currently, locally prevalent, a female recruits the genetic basis for that resistance for her offspring. This theory has now garnered extensive support in a wide range of vertebrate and invertebrate taxa, including comparative demonstrations that species with higher pathogen loads have more elaborate sexual ornaments than related species under lesser pathogen pressure (see, e.g., [Read \(1988\)](#)); demonstrations that the ornaments to which females attend indeed provide evidence of a male's disease history or current pathogen loads, and (in some cases) that females actually pay the most attention to the traits that are most informative in this regard (see, e.g., [Zuk et al. \(1990a,b\)](#)); and demonstrations that females who are permitted to choose their mates indeed produce offspring that are more disease resistant than those of females who are assigned a mate and cannot choose ([Drickamer et al., 2000](#); [Johnsen et al., 2000](#)).

A long-standing puzzle about courtship displays is why, if a signal such as a bright ornament or a song of some particular quality is attractive to females, do all males not display it. The answer seems to be that selection on the recipients of signals favors attending only to honest signals that are genuinely informative and ignoring those that an impostor is capable of faking ([Grafen, 1990](#); [Zahavi and Zahavi, 1997](#); [Johnstone, 1995](#)). One consideration that apparently constrains

the ability of low-quality males to cheat by displaying T-dependent ornaments is that T suppresses the immune system ([Wichmann et al., 1997](#); [Angele et al., 1998](#); [Yao et al., 2003](#)), making males with high T-levels more vulnerable to infections (see, e.g., [Folstad and Karter \(1992\)](#), [Thompson et al. \(1997\)](#), and [Kacelnik and Norris \(1998\)](#)). Males with high-energy reserves, no wounds, and genotypes that are relatively resistant to local pathogen strains can presumably afford the immunosuppression that developing and maintaining ornaments requires, when other males cannot. (Why ornaments should not then evolve to no longer be androgen dependent, so that males who can develop them without paying these costs can invade the population, is another puzzle. Perhaps this does happen to different ornaments in different evolving lineages, and females are then selected to ignore the signal, contributing to the taxonomic diversification of display features.)

The essence of the immunocompetence hypothesis is that males invest in the production of the secondary sexual traits that females prefer to the degree that they are of sufficient intrinsic quality and/or in sufficiently good condition to tolerate the associated costs, especially that of compromising their immune system ([Folstad and Karter, 1992](#)). The several elements of this argument have seldom been empirically demonstrated in a single system, but research on the red jungle fowl (*Gallus gallus*), the ancestor of the domestic hen, comes close. Females have been shown to prefer males with the largest and brightest ornaments, and to pay the greatest attention to the ornaments that respond most to the male's disease history ([Ligon et al., 1990](#); [Zuk et al., 1990a,b](#)). One of the most important male attributes for female choice is the size of the comb, which has been shown to be positively correlated with T-levels ([Zuk et al., 1995](#); [Verhulst et al., 1999](#)). Furthermore, immune response is negatively correlated with both T-levels and the size of the comb, a remarkable demonstration that the relatively vigorous and decorated cocks that hens prefer are indeed paying a price. However, relationships among T, immune response, and secondary sexual traits are not always this consistent with the immunocompetence hypothesis in other species ([Hasselquist et al., 1999](#); [Ros et al., 1997](#); [Weatherhead et al., 1993](#)) and evidence in support of the specific premise that developing T-dependent traits imposes an immunocompetence cost is mixed and needs to be interpreted with caution ([Roberts et al., 2004](#)). But the costs that keep T-dependent signals honest need not reflect direct immunosuppressive effects;

they may instead be mediated by other correlated factors, such as lipid stores and leptin levels (Alonso-Alvarez et al., 2007a), or by T's effects on such things as antioxidant activity (Alonso-Alvarez et al., 2007b), and carotenoid deposition (Blas et al., 2006). Ongoing studies should help identify important modulating variables and clarify whether the diverse findings to date can be encompassed under a single theory.

A difficulty in testing the immunocompetence hypothesis is that even where it is correct, different relationships between secondary sexual traits and immune response may be observed. High-quality males can sometimes afford T's negative effects on their immune systems precisely because they still perform better than those of low-quality males, in which case the correlation will still be positive. In such cases, it may be most informative to compare males after administering both exogenous T and an immune challenge, eliminating the confound between T-levels and male quality (see, e.g., Ros et al. (1997)). A correlation between ornamentation and immune response in males whose T-levels have not been experimentally manipulated is likely to reflect variation in allocation between current reproductive effort and its alternative, somatic effort (growth and maintenance), which can be considered an investment in future reproduction. Stickleback (*Gasterosteus aculeatus*) males invest in the pigmentation that makes them attractive to females (reproductive effort) when in good condition (indexed by lipid stores), as one might expect, but also do so when in especially poor condition or in the presence of a predator (Candolin, 1998, 1999); it appears that males in the best condition find the prospective fitness benefits of reproductive effort sufficient to cover the costs and those in somewhat poorer condition do not, but those in the worst condition give up on future reproduction altogether, in response to cues indicating that they are unlikely to get another chance (Candolin, 1998, 1999; Kokko, 1997). From a female perspective, such males who invest everything in a last-ditch mating effort are dishonest signalers, and selection may be expected to favor females who are able to detect quality cues that cannot be faked, so there is male–female conflict in these cases, and a potential for evolutionary arms races.

Males with high T-levels incur other costs in addition to immunosuppression. Their basal metabolic rate may be elevated (Buchanan et al., 2001), and the behavioral risk taking that creates mating opportunities can also increase the chance of injury

in an aggressive contest and of falling victim to a predator (see, e.g., Daly et al. (1990)). The upshot is that a male whose blood T increases may gain in reproductive success, but risks shortening his life and there is evidence for this occurring in humans (Hamilton, 1948; Hamilton and Mestler, 1969; but see also Nieschlag et al. (1993)) and in nonhuman species (Wingfield et al., 1997; Dufty, 1989). Moreover, as we have already noted, T enhances mating effort at the expense of paternal investment (Raouf et al., 1997; Wingfield et al., 1997) so that even apart from the energetic and mortality costs, T may have simultaneous opposing effects on different components of fitness. The optimal level of circulating T for a male is clearly both species specific and a complex function of his individual situation and attributes.

### 89.3 Concluding Remarks

The psychophysiological controls and behavioral manifestations of intrasexual competition have undoubtedly been shaped by a history of sexual selection. This implies that perceptual and cognitive mechanisms subserving interpretation of social situations and decision making must be functionally integrated with endocrine, immune, and other physiological systems to produce coordinated and subtly modulated responses to cues of the utility of competitive and aggressive inclinations and actions, at least as they would have paid off in fitness in ancestral environments. We have proposed that dangerous competitive violence is modulated by cues of one's social and material circumstances, both absolute and relative, and by some sort of mental model of the current local utility of competitive success. An evolutionary psychological perspective can help direct research on psychophysiological mechanisms by identifying the sorts of contingent response that are likely to have been favored by selection, and is equally of relevance for the social sciences, by suggesting hypotheses about the probable impacts of social factors such as inequitable resource distributions.

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## Biographical Sketch



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