Contents lists available at ScienceDirect

Aggression and Violent Behavior



Homicide adaptations

Joshua D. Duntley *, David M. Buss

Richard Stockton College, University of Texas, Austin, United States

ARTICLE INFO

Article history: Received 11 April 2011 Received in revised form 26 April 2011 Accepted 27 April 2011 Available online 5 May 2011

Keywords: Homicide Adaptation Theory Evolutionary psychology Homicide Lethal aggression

Contents

ABSTRACT

We propose Homicide Adaptation Theory as a new explanation for why people kill. Multiple homicide mechanisms have evolved as effective context-sensitive solutions to distinct adaptive problems. Killing historically conferred large fitness benefits: preventing premature death, removing cost-inflicting rivals, gaining resources, aborting rivals' prenatal offspring, eliminating stepchildren, and winnowing future competitors of one's children. Homicidal ideation is part of evolved psychological design for killing, functioning to mobilize attention, rehearse scenarios, calculate consequences, and motivate behavior. Because being killed inflicts temporally cascading costs on victims, selection has forged death-prevention strategies, producing co-evolutionary arms races between homicidal strategies and anti-homicide defenses.

© 2011 Elsevier Ltd. All rights reserved.

1.		400
2.	Previous evolutionary theories of homicide	400
3.	Homicide Adaptation Theory	400
4.	Sex differences in homicide mechanisms	401
5.	Infanticide	402
6	In what contexts will people kill instead of doing something else?	403
7	Fitness costs of being killed	403
9. Q	Consultion of being kinetic	103
o. 0		403
9.	vicum defenses against nomicide	404
10.	Unique design features of psychological adaptations for homicide.	404
	10.1. Sensitive to adaptive problems solvable by homicide	405
	10.2. Catalog homicide-relevant information	405
	10.3. Estimate formidability of victims	405
	10.4 Forecast likely consequences of murder	405
	105 Cognitively simulate killing	406
	10.5 Uppertrainty	100
		400
11.	Evidence.	407
12.	Limitations and future directions	408
13.	Conclusion	408
Refere	nces	409

The murder of an individual or his close kin are among the greatest costs that can be inflicted on any individual. The dead cease to contribute to their own affairs and cannot actively influence the affairs of their families, friends, or enemies. Wherever written laws exist, killing is always singled out as a crime. No other infraction comes attached with greater punishment. Where written laws are absent, killing typically constitutes a major cause of death, sometimes accounting for the mortality of a third of all males (Keeley, 1996). Although cultures with written laws, hired police forces, and the prospect of imprisonment have substantially lower homicide rates than cultures lacking them the lifetime odds of dying by the hand of another in modern societies run as high as one in twenty-six for certain sub-groups, such as inner-city males (Ghiglieri, 1999).

In this paper, we review data on patterns of homicide in the United States and around the world. We introduce our evolutionary theory of homicide and discuss how adaptationist logic can both explain



^{*} Corresponding author at: Social and Behavioral Sciences, Richard Stockton College, Pomona, NJ 08240, United States.

E-mail address: joshua.duntley@stockton.edu (J.D. Duntley).

^{1359-1789/\$ –} see front matter 0 2011 Elsevier Ltd. All rights reserved. doi:10.1016/j.avb.2011.04.016

existing findings on homicide and lead to novel predictions. We explore the costs of being a victim of lethal aggression and explain how adaptations that produce homicide and adaptations that defend against being killed are locked in an antagonistic coevolutionary arms race. Finally, we explore evidence supporting Homicide Adaptation Theory.

1. Homicide prevalence

13,636 people were victims of homicide in the United States in 2009 (FBI, 2010a). This converts to a homicide rate of 4.5 out of 100,000 people for that year. With an average lifespan of 78 years in the United States in 2009 (World Bank, 2009), the lifetime risk of being a homicide victim is 1 in 287. According to Federal Bureau of Investigation (2010) homicide data, at least 78.5% of homicide victims in 2009 were male.

Given the prevalence of homicide and the dramatic nature of its consequences, it may seem astonishing to realize that "we have only the most rudimentary scientific understanding of who is likely to kill whom and why" (Daly & Wilson, 1988, p. ix). For our understanding of homicide to be complete, we must explain, at a minimum: (1) why men are vastly over-represented among killers (87%); (2) why men are also over-represented among victims (75%); (3) why women commit some kinds of homicide more than men, such as infanticide of their own children; (4) why predictable motives for murder lead people to kill in qualitatively distinct conditions; and (5) why people experience homicidal fantasies in circumstances that turn out to correspond closely to the contexts in which people actually commit murder.

2. Previous evolutionary theories of homicide

Over the past few decades, several evolutionary scientists have offered explanations for homicide. Almost without exception, however, the evolutionary hypotheses posit killing as unnatural and not part of our evolved psychology. The ethologist Eibl-Eibesfeldt (1989), for example, proposed that killing (e.g., in war) is a culturally imposed behavior that overrides an innate human inhibition to kill. Killing, according to this view, is a cultural aberration and in no way part of human evolved psychology. This explanation leads to no detailed predictions about the various forms of homicide or about the contexts in which they occur.

The most comprehensive evolutionary explanation specifically advanced to account for patterns of homicide to date was proposed by Daly and Wilson (1988, 1989, 1998, 1999). Daly and Wilson have made pioneering contributions to our understanding of homicide and the contexts in which it occurs. They advance two distinct arguments about homicide. In the first argument, Daly and Wilson are agnostic about whether there are adaptations designed to produce homicide, "... our evolutionary psychological approach in no way depends upon homicide per se being 'an adaptation.' It may or may not be the case that actual killing was a regular component of the selective events that shaped human passions" (Daly & Wilson, 1988, p. 12). This position is expressed again in another publication: "Using homicides as a sort of 'assay' of the evolved psychology of interpersonal conflict does not presuppose that killing per se is or ever was adaptive" (Wilson, Daly, & Daniele, 1995).

In the same publications, Daly & Wilson also advance the view that humans do not have an evolved psychology of homicide. Rather, they propose that homicides can be viewed as "dysfunctionally extreme byproducts," "epiphenomena", or "overreactive mistakes" of evolved mechanisms designed for their non-lethal outcomes. This is a kind of "spandrels" or byproduct argument (see Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Gould, 1991). According to this argument, "It is quite possible that actually killing one's antagonist is more often than not an overreactive *mistake*—an act with negative consequences both for the killer's net hedonic utility and for the actual expected fitness of which that utility is an evolved token" (Daly & Wilson, 1998, p. 438, italics original). These arguments illustrate that Daly and Wilson explicitly are not proposing that humans have evolved distinct adaptations for homicide, although they do not rule out the possibility completely.

Subsequent evolutionary psychologists have adopted Daly and Wilson's position (e.g., Crabb, 2000; Kenrick & Sheets, 1993). Crabb, for example, argues that "psychological machinery for aggressive impulses would have served inclusive fitness well, with the caveat that extreme aggression leading to homicide may be disastrous for inclusive fitness because it may result in fatal retribution against the perpetrator" (Crabb, 2000, p. 226).

Although Daly, Wilson, and colleagues do not propose that humans have evolved psychological mechanisms specialized for killing, they do emphasize the importance and priority of an evolutionary psychological explanatory account: "... what is needed is a Darwinian psychology that uses evolutionary ideas as a metatheory for the postulation of cognitive/emotional/motivational mechanisms and strategies" (Daly & Wilson, 1989, p. 108–109).

We agree with Daly and Wilson that some homicides are byproducts of the operation of evolved mechanisms designed for non-lethal outcomes, such as coercion and control. However, we suggest that these represent a minority of killings. We propose that most killings are better explained as the designed products of adaptations selected specifically for their lethal outcomes.

3. Homicide Adaptation Theory

By advancing Homicide Adaptation Theory, we propose that there have been highly specific and recurrent contexts over human evolutionary history in which the fitness benefits of killing outweighed the fitness costs. These contexts are defined by distinct adaptive problems for which murder was one effective solution among several potential other, non-lethal solutions. Examples of these adaptive problems include self-defense, kin protection, curtailing the costs of investing in genetically unrelated individuals, curtailing the costs of investing in a genetically related individual with poor survival and reproductive prospects, acquisition of reproductively relevant resources, acquisition of new mates, and the elimination of a cost-inflicting rival. We propose that humans have evolved distinct, context-sensitive psychological mechanisms that determine whether homicide or a non-lethal adaptive solution will be implemented. We propose that these mechanisms are activated by a delimited set of circumstances, and that they are designed to produce the death of conspecifics.

A host of beneficial consequences, in the currency of fitness, historically flowed to killers as a result of murdering in some contexts (Buss & Duntley, 1998, 1999; 2003; 2006; Duntley, 2005; Duntley & Buss, 1998, 1999, 2005, 2008). Although some homicides may be caused by accidents, incidental byproducts of other evolved mechanisms, pathology, or necessary costs of brinksmanship, many or most killings, according to Homicide Adaptation Theory, are murders by design—killings generated by psychological adaptations whose function is to produce conspecific death.

Homicide is such a unique and potentially powerful strategy with dramatic fitness consequences for both perpetrator and victim that it is reasonable to hypothesize that it has been subjected to evolution by natural and sexual selection. Homicide is different from non-lethal strategies for inflicting costs because it leads to the absolute end of direct competition between two individuals. The person who is killed can no longer compete with his killer. A dead competitor can no longer directly influence the environment or social context that he shared with his killer. The distinct outcomes of homicide would have created equally unique selection pressures to shape human psychology specifically for contexts of homicide (Buss & Duntley, under review; Duntley, 2005; Duntley & Buss, 2008).

There would have been, in principle, many potential fitness related benefits of killing another human being over human evolutionary history. The particular benefits reaped as a result of killing undoubtedly varied with the nature of the person killed, their relationship to the killer, the social context, and the personal circumstances of the killer and victim. Specifically, the killing of a conspecific could have contributed to:

- (a) Eliminating a cost-inflicting intrasexual competitor;
- (b) Gaining access to rivals' reproductively relevant resources;
- (c) Gaining access to fertile mates;
- (d) Creating and managing a reputation that deters exploitation, reducing costs inflicted by rivals;
- (e) Preventing the exploitation, injury, rape, or killing of self, kin, mates, and coalitional allies by conspecifics in the present and future;
- (f) Protecting resources, territory, shelter, and food from competitors;
- (g) Eliminating resource-absorbing or costly individuals who are not genetically related (e.g., stepchildren);
- (h) Eliminating genetic relatives who interfere with investment in other vehicles better able to translate resource investment into genetic fitness (e.g., deformed infants, the chronically ill or infirm).

These are a sample of direct fitness benefits that could have flowed to ancestral human killers. These benefits would not always, necessarily, or even frequently have flowed to killers as a consequence of killing. On the contrary, we propose that evolved defenses against being killed have made the costs of a homicidal strategy prohibitively high in many circumstances. However, the potential fitness benefits of conspecific killing are so large in number and substantial that there is no a priori reason to be skeptical about the possibility that homicidal adaptations could have evolved.

By attempting to kill someone, the would-be killer risks getting injured or killed. Because killing has been a recurrent selective force, humans have evolved anti-homicide adaptations designed to prevent being killed. In many cases, these adaptations are designed to inflict costs on would-be killers to deter them from killing. Successful homicides may provoke costly retaliation by the victim's kin, friends, or mates, inflicting damage or death on the killer. Some killers risk ostracism, reputational damage, status loss, or damage to mate value that interferes with the successful accomplishment of tasks such as surviving, mating, and investing in children. These substantial costs historically would have deterred, and presently continue to deter many would-be killers.

In short, we view the common intuition that killing is a dangerous and potential costly strategy for killers as essentially correct precisely because humans have evolved such sophisticated adaptations for preventing being killed. According to our theory, homicide rates would be far higher without the evolution of anti-homicide defenses. At the same time, evidence for the existence of anti-homicide defenses provides powerful evidence that murder by other humans was indeed a recurrent hazard over human evolutionary history.

We propose that adaptations for homicide would be more likely to evolve when they reliably contributed to the solution of an adaptive problem with a high impact on individual fitness, such as preventing a rival from killing one's child. Adaptations for homicide also would be more likely to evolve when a large number of different adaptive problems could be solved simultaneously, or at least partially solved, by adopting a homicidal strategy. Consider, for example, the intrasexual rival of a man who is preventing the man's ascension in a status hierarchy, attempting to poach away the his mate, monopolizing a scarce and valuable shelter as winter approaches, and who takes every opportunity to publicly humiliate the man's brother. Killing the rival has the potential to contribute to the solution of each of these adaptive problems. The greater the fitness costs that a rival imposes on an individual, the more selection would favor the evolution of homicidal strategies to eliminate the rival.

The adaptive problems for which the fitness benefits of killing outweighed the fitness costs, on average, were many in number and distinct in nature. Different ancestral problems required different specific solutions. Homicide Adaptation Theory proposes that there are multiple, different psychological adaptations for homicide, each of which is devoted to the solution of different domains of adaptive problems. For example, psychological design for infanticide by men who suspect or know that the infant is not his own differs from psychological design for infanticide by young women who produce a deformed infant who would have been unlikely to survive and thrive in ancestral conditions. Psychological design for intrasexual rivalry homicide in men prompted by a mate poacher differs from psychological design for coalitional warfare.

Of course, some information processing mechanisms are undoubtedly shared between the different adaptations for homicide and adaptations for different behavioral solutions. However, to qualify as a distinct adaptation, any given adaptation for homicide must have at least one design feature not shared by other adaptations. Each must also have at least one distinct function not shared with other adaptations that correspond to the specific benefits, or specific reductions in costs, that killers would have accrued in each context.

It is critical to note that Homicide Adaptation Theory does *not* imply that homicide will be the *preferred* strategy for any particular adaptive problem in all, or even in most, situations, broadly defined. In most circumstances, the high costs of committing homicide would have outweighed its benefits precisely because of the existence of evolved anti-homicide adaptations. The theory does propose that homicidal behavior was the best solution for at least some combinations of adaptive problems and circumstances, which provided selection pressure for the evolution of homicide adaptations.

4. Sex differences in homicide mechanisms

We hypothesize that selection has shaped separate homicide mechanisms in men and women. The overwhelming majority of homicides are committed by men. It should not be surprising that men, not women, have evolved bodies and minds designed to kill. We propose that men have evolved some homicidal mechanisms that women lack, such as those designed for warfare (see also, Tooby & Cosmides, 1988; 2010; Wrangham, 1999), and that women evolved some homicidal mechanisms men lack, such as those designed to produce spontaneous abortion and certain types of infanticide.

For a young woman, the fetus she carries rarely represents her last opportunity to reproduce. Women were selected to invest more in those offspring who will yield the greater reproductive benefit, even in utero. If a fetus is not viable, it would make more sense for a pregnant woman to forgo her investment in its development in favor of investing in a subsequent pregnancy. Most fertilized eggs do not result in a full-term pregnancy. Up to 78% fail to implant or are spontaneously aborted (Nesse & Williams, 1994). Most often, these outcomes occur because the mother detects chromosomal abnormalities in the fetus. The mother's ability to detect such abnormalities is the result of adaptations that function to prevent the mother from investing in offspring that likely will die young. Most miscarriages occur during the first trimester (Haig, 1993), at a point when the mother has not yet invested heavily in a costly pregnancy and the spontaneously aborted fetus is less likely to lead to infection (Saraiya et al., 1999). It however, is not a passive pawn in its mother's evolved reproductive strategy. It has only one chance to live. Selection would have favored fetal genes to resist its mother's attempt to abort it. The production and release of human chorionic gonadotropin (hCG) by the fetus into the mother's bloodstream, which is normally an honest signal of fetal viability, may be one adaptation against being spontaneously aborted. The hormone prevents the mother from menstruating, allowing the fetus to remain implanted. Maternal

physiology reacts to the production of hCG as a sign that the developing fetus is viable (Haig, 1993). In short, women seem to have adaptations to kill their own fetuses—adaptations clearly lacking in men.

Even when men and women both possess homicide mechanisms that produce the same outcome (e.g., both sexes have evolved mechanisms to kill infants), some design features of the mechanisms differ. For example, we propose that only men are sensitive to paternity uncertainty and only women are sensitive to the lack of an investing father. The mechanisms may function through different inhibitory thresholds for the same type of killing (see Campbell, 1999), or may be implemented in entirely distinct adaptations.

Some hypothesized sex differences have a straightforward evolutionary logic that has been articulated by others in the context of violence (e.g., Daly & Wilson, 1988; Ellison, 1985). Men and women face some different adaptive problems of mating. For example, women's typical minimum obligatory investment in reproduction is 9 months, longer if the period of breast feeding is included. Men, in contrast, can invest as little as a few hours or a few minutes to produce the same child that requires months or years of investment from women. Because women's minimum obligatory investment in reproduction is greater, the costs of a poor mate choice are greater for women than for men (Trivers, 1972). As a result, women tend to be choosier when selecting mates in short-term mating contexts where the discrepancy in parental investment between the sexes is greater.

There is also conflict between the sexes about the timing of sexual activity, or indeed whether sex occurs at all with a particular partner. Because sex is less costly for men than for women, men tend to desire sex earlier in romantic relationships, and with less investment, than do women (Werner-Wilson, 1998). Men also desire a greater number of sexual partners than do women (Schmitt, Shackelford, Duntely, Tooke, & Buss, 2001) and are more inclined to short-term, uncommitted sex (Buss, 2003; Buss & Schmitt, 2011).

Women are biologically limited in the number of offspring they can bear in their lifetime. Once a woman is pregnant, additional sex partners will not lead her to have additional offspring. For men, however, shortterm sex with multiple partners can lead to additional offspring. Men's rate of reproduction is limited primarily by the number of females they can impregnate. Given an equal sex ratio in the mating pool, men who impregnate more than one woman or who have more than one longterm partner at any time effectively deprive other men of mates. Competition between men over mating opportunities with women is a central source of conflict in the fitness interests of male rivals.

Human polygynous mating systems, in which some males may have more than one mate at a time, lead to greater reproductive success for the polygynous men and zero reproductive success for many of their competitors. Over evolutionary time, the greater reproductive variance among men selected for more extreme and risky male strategies to acquire and retain mates. Daly and Wilson (1988) argue that sex differences in the use of risky strategies, such as violence and homicide, are an outcome of this unique selection pressure on men. Over evolutionary time, men who failed to take risks would have been at a disadvantage in competition for mates and, therefore, less likely to leave descendants (Daly & Wilson, 1988; Kruger & Nesse, 2004; Wilson & Daly, 1985).

Fitness conflicts between the sexes also result from the fact that fertilization occurs internally within women. As a result, women are always certain that the offspring that they bear are genetically related to them. Men, however, are always less than certain of their paternity (Buss, 2003; Symons, 1979). Men's paternity uncertainty has been proposed to be the primary selective impetus for the finding that men's jealousy, more than women's jealousy, centers on the sexual aspects of a partner's infidelity (Buss & Haselton, 2005; Buss, Larsen, Westen, & Semmelroth, 1992).

In the ancestral past, men and women also differed in the greatest threats to their long-term romantic relationships. A partner's sexual infidelity was more costly for men who could then invest limited resources in another man's child rather than their own. A partner's emotional infidelity was more costly for women who may suffer a decrease or loss of their male partner's investment that could be critical for the women's survival and that of their dependent children. Sex differences in the costs of threats to long-term romantic relationships are hypothesized to have selected for more costinflicting behaviors perpetrated by men in response to contexts of sexual infidelity and more cost-inflicting behaviors perpetrated by women in response to contexts of emotional infidelity. Both men and women may use cost-inflicting behaviors to address each of the fitness conflicts discussed. However, across contexts in which women utilize cost-inflicting behaviors, we hypothesize that they will be less risky than those used by men. In the next section we explore infanticide in greater detail to illustrate the utility of our adaptationist theory for understanding sex differences in patterns of homicide. For a complete discussion of the full range of contexts of homicide, refer to Buss and Duntley (under review).

5. Infanticide

Compared to men, women's fertile years are confined to a smaller portion of their lifespan. Given the small number of children a woman can produce, we propose that selection forged mechanisms to terminate maternal investment in some infants in order to preserve her finite time and resources for others.

There are five adaptive problems that we propose infanticide solved for ancestral women. These include:

- avoiding investment in physically sub-par offspring who were unlikely to convert parental resources into their own reproductive success (e.g., those who were deformed, diseased)
- (2) avoiding investment in offspring when external conditions hampered the infant's survival (e.g., food scarcity, lack of an investing father, harsh season)
- (3) eliminating competition for older or more viable offspring when resources were scarce (e.g., twin births or when birth spacing was too close).

Infanticide would have solved different problems for males than for females. Consequently, the contexts in which men and women kill infants should differ. For example, having children with a former mate does not decrease the mate value of a man as much as for a woman (Buss, 2003). And killing a sub-par infant usually would not free as much of a man's resources because men typically invest less than women in parenting. Hence, we predict that men should be *less* likely than women to kill their own sub-par infants.

There are, however, several adaptive problems solved by maleperpetrated infanticide that we hypothesize were ancestrally recurrent and weaker or entirely absent in women. These include:

- avoiding investment in a rival male's infant (e.g., mate was already pregnant prior to the initiation of the current mateship)
- (2) terminating investment in an infant for whom there is paternity uncertainty (e.g., appraisal of possible infidelity by the woman)
- (3) preventing the man's mate from investing in an offspring that is not optimal for him, leaving her to invest in the man's current or future offspring instead
- (4) hastening the mate's ovulation and hence conceptability: since breastfeeding tends to produce anovulatory cycles, eliminating an infant dependent on breastfeeding will hasten ovulation in the woman.

Daly and Wilson (1988) present evidence suggesting that parents kill their infants under predictable circumstances that support the general logic of our hypotheses, including: (a) fathers killing when there is paternal uncertainty, such that the infant might not be the putative father's child; (b) mothers killing when the infant is

deformed, diseased, severely underweight, or of otherwise questionable quality, such that it might not survive or thrive; and (c) mothers killing when external circumstances, such as food scarcity or lack of an investing father, render the timing unpropitious for a woman to reproduce. Although Daly and Wilson do not interpret these findings as evidence for infanticide adaptations, we believe that the crosscultural ubiquity of these findings provides compelling evidence of "special design" for such adaptations.

6. In what contexts will people kill instead of doing something else?

Research that attempts to empirically examine what factors lead some to adopt strategies of non-lethal aggression and others to kill is scarce. In one recent example, a study of male violence directed toward female intimate partners found that, relative to abusers, men who killed had more conventional childhoods, education, employment, and criminal careers (Dobash, Dobash, Cavanagh, & Medina-Ariza, 2007). Males who killed their intimate partners were also more likely to be possessive and jealous of them. Consistent with Daly and Wilson's (1988) findings, Dobash et al., (2007) found that when men killed, they were more likely to be separated from their partner. Men who killed were also more likely to have used violence against a previous partner and to have sexually assaulted and strangled the victim. Interestingly, men who killed were less likely to have been drunk at the time of the homicide or to have previously used violence against the woman they killed, suggesting that a pattern of non-lethal aggression with a particular partner is not usually predictive of her eventual homicide.

These research findings draw attention to a difficulty in predicting when homicide rather than non-lethal aggression will occur. It is not possible to point to features of a situation or adaptive problem context that will reliably lead to homicide in every instance, in every person. With our current state of understanding, the best we can do is identify factors associated with an increased probability of lethal aggression. There are mitigating environmental factors (Gartner, 1990), hormonal influences (Niehoff, 1999), life history influences (Kaplan & Gangestad, 2005), the developmental calibration of psychological mechanisms (Dodge, Bates, & Pettit, 1990), and heritable personality features (Rhee & Waldman, 2002) that influence behavior. The activation threshold of homicide adaptations could be especially lower among a subset of the male population high in a particular heritable personality traitpsychopathy (Lalumière, Mishra, & Harris, 2008; Mealey, 1995; Pitchford, 2001; also see Glenn, Kurzban, & Raine, in press). Many or all of these sources of individual differences were part of the selection pressures that shaped homicide adaptations. Thus, a combination of cues to the presence of an adaptive problem ancestrally solvable by conspecific killing activates homicide adaptations. The presence of these cues, as well as their magnitude, can help us to predict when conspecific killing will be more or less likely to occur. Without complete knowledge of how human psychology produces homicidal behavior, however, it is not possible to make perfect predictions about whether homicide will occur in an individual case. The same is true of making predictions about any behavior.

7. Fitness costs of being killed

Whether there are adaptations specifically for homicide, conspecific killing was a recurrent feature of human evolutionary history (Chagnon, 1988; Trinkaus & Shipman, 1993). Examining the costs of homicide through an evolutionary lens elucidates the nature and magnitude of the costs incurred by victims of homicide, and gives us a better understanding of how other humans were significant dangers over our evolutionary history. A victim's death has a much larger impact on his or her inclusive fitness than the loss of the genes housed in the person's body. The inclusive fitness costs of dying at the hands of another human can cascade to the victim's children, spouse, kin, and coalitional allies. The specific costs include:

Loss of future reproduction. A victim of homicide cannot reproduce in the future with a current mate or with other possible mates. On average, this cost would have been greater for younger individuals than for older individuals.

Damage to existing children. The child of a murdered parent receives fewer resources, is more susceptible to being exploited by others, and may have more difficulty ascending status hierarchies or negotiating mating relationships, which will likely lead to poorer fitness outcomes. Children of a murdered parent may see their surviving parent's investment diverted away from them to a new mating relationship and to the children who are the product of that relationship (Geary, 2000). A single parent, who can invest less than what two parents can invest, might abandon his or her children in favor of better mating prospects in the future. And the children of a murdered parent risk becoming stepchildren, a condition that brings with it physical abuse and homicide rates 40 to 100 times greater than those found for children who reside with two genetic parents (Daly & Wilson, 1988).

Damage to extended kin group. A homicide victim cannot protect or invest in kin. A victim's entire kin network can gain the reputation of being vulnerable to exploitation as a result of the person's death. A homicide victim cannot influence the status trajectories or mating relationships of family members. And the open position left by the victim in a kin network's status hierarchy could create a struggle for power among the surviving family members.

Homicide victim's fitness losses can be rival's fitness gains. Killers can benefit from the residual reproductive value and parenting value of the surviving mate of their victim, sometimes at the expense of the victim's children with that mate. A killer can ascend into the vacancy in a status hierarchy left by his victim. The children of killers would thrive relative to the children of homicide victims, who would be deprived of the investment, protection, and influence of a genetic parent. Many family members who would have survived if the person was not killed will die before they can reproduce. And many children who would have been born to members of the family will never be born.

The magnitude of rivals' fitness gains will be heavily dependent on group size. In smaller groups, a slight local increase in resources or mates, following a murder, can bring a substantial benefit to the murderer. In larger groups, however, the fitness benefits could be diluted because the newly available resources could be harder to keep from the hands of the larger number of competitors.

8. Co-evolution of homicide and anti-homicide

Homicide victims incur large, multiple, and previously theoretically unrecognized fitness costs that cascade to their children, grandchildren, and entire kin group. Although it would certainly not make headlines to announce that it's costly to be killed, being a homicide victim has fitness consequences that no prior theories of homicide or human survival have enumerated or illuminated.

The principle of co-evolution typically has been used to describe reciprocal evolutionary changes in interacting species, such as predators and prey or parasites and hosts. It has been used less often to explain reciprocal evolutionary changes within a single species, although there are important exceptions to this generalization (e.g., Buss, 2000; Haig, 1993; Holland & Rice, 1998). Just as killers obtained large ancestral benefits from the use of homicide in some contexts, victims and their genetic kin suffered extraordinary costs. The costs are hypothesized to have created selection pressure for the evolution of defenses against becoming a victim of homicide and for adaptations in victims' genetic kin to prevent relatives' untimely deaths or minimize their costs. The evolution of defenses against lethal aggression would have created new selection pressure on adaptations for homicide, shaping new design features capable of bypassing victims' defenses. This coevolutionary arms race between homicide adaptations and victim defenses is hypothesized to have contributed to rapid evolutionary change and corresponding design features in both (see Fig. 1).

9. Victim defenses against homicide

If homicide recurred in predictable contexts over our evolutionary history, it would have created selection pressures to avoid being killed in precisely those contexts. We propose that the selection pressures created by the costs of being killed were powerful enough to shape distinct adaptations to defend against homicide (Duntley & Buss, 1998; 2000; 2001; 2002; Buss & Duntley, under review).

The strength of selection for any adaptation, including defenses against being killed, is a function of the *frequency* of the event and the *net fitness benefits* of the event relative to the frequency and net benefits of other, competing strategies in the population at the same time. Low base-rate events that impose heavy fitness costs, like homicide, can create intense selection pressures for adaptations to prevent or to avoid them. Ancestral homicides, however, may not have been as infrequent as they are in many modern societies. Homicide rates in hunter–gatherer societies, which more closely resemble the conditions in which humans evolved, are far higher than those in modern nations with organized judicial systems (Ghiglieri, 1999; Marshall & Block, 2004).

In sum, Homicide Adaptation Theory proposes a new explanation for why people kill other humans: Over the long expanse of human history, there were recurrent sources of conflict between individuals, such as conflict over reputation and social status, conflict over resources, and conflict over romantic partners. Killing is hypothesized to be one among an arsenal of context-contingent strategies shaped by natural selection to win conflicts with others. Homicide differs qualitatively from nonlethal solutions to conflict. Once dead, a person can no longer damage the killer's reputation, steal his resources, prevent the killer from attracting a romantic partner, or have sex with the killer's spouse. According to Homicide Adaptation Theory, our



Fig. 1. Antagonistic coevolution: killer adaptations and evolved anti-homicide defenses.

evolutionary heritage has endowed all of us with a psychology to kill others. These psychological processes lead us to entertain fantasies of killing and, in rare instances, act on them when we encounter sources of conflict that were successfully won by homicide in the evolutionary past.

Selection would have favored individuals who possessed psychological adaptations that reliably led to the production of homicidal behavior when they faced such contexts. The best solution to most adaptive problem contexts faced by our ancestors did not involve homicide. However, the potential fitness gains accomplished by the use of killing to solve some adaptive problems in delimited contextspecific conditions would have selected for psychological adaptations for homicide.

Homicide Adaptation Theory argues that psychological mechanisms for homicide steer an individual in the direction of adaptive behaviors that reliably result in the death of another individual. This is accomplished through a variety of affective, motivational, and computational systems that narrow in on homicide as the solution to adaptive problems. The adaptive problems to which we are referring are dynamic. As time passes and other individuals pursue adaptive strategies, the nature of adaptive problems change, and the solution to one set of adaptive problems may reliably create others. Reliable patterns in the unfolding of adaptive problems is what shaped psychological adaptations in humans over evolutionary time, including those that end others' lives.

10. Unique design features of psychological adaptations for homicide

Thoughts of killing conspecifics are proposed to be part of larger information processing circuits that evaluate the appropriateness of several different behavioral strategies for dealing with a particular adaptive problem before implementing any one course of action. Homicidal thoughts have multiple proposed functions, such as making credible threats, exploring the possibility of homicide, motivating actual homicides, and inhibiting homicidal behavior when the costs outweigh the benefits. Homicide as a chosen strategy differs from all other behavioral strategies in that it results in the abrupt and permanent end of direct competition with another individual. For this reason, we propose that the information processing biases for considering homicide evolved to differ from the information processing utilized in the consideration of non-lethal strategies in several important ways. First, unlike non-lethal aggression, homicide is a behavior that, under some circumstances, will leave no witnesses other than the killer. We propose that people are quite good at identifying who had a motive to kill and can rapidly reduce the list of suspects. It was likely the case in ancestral conditions that most killings would not have been anonymous. However, without witnesses, a killer has at least some plausible deniability of involvement in the death of a rival, especially in ancestral environments. This would have decreased the average likelihood that kin or social allies of the victim would seek retribution. As a result, selection is hypothesized to have shaped mechanisms for murder in some contexts to be sensitive to others' perceptions that the killer would have a motive and the presence of witnesses, and motivate homicidal behavior more frequently when they are absent.

An exception to this prediction is homicide committed to defend status and reputation that occurs in response to some form of public challenge or humiliation. The "public" element of this kind of threat to reputation is a key component of the adaptive problem. We hypothesize that for murder to be an effective solution in many such contexts, the killing should be enacted in front of witnesses. A public challenge that can be immediately resolved by one of the parties involved will often garner greater reputational benefits than a response occurring at a later time in an unrelated context. There are clear time limits on the effectiveness of strategies for seeking revenge, including homicide. Waiting too long to avenge being wronged can decrease the effectiveness of vengeance in two ways: First by allowing more time for a reputation of being exploitable to grow, and second by creating a larger window for exploitation to occur. Killing the individual who is the source of reputational damage is one effective strategy for the defense of reputation (Buss, 2005; Chagnon, 1988). Murder eliminates the person's ability to inflict costs in the future and clearly signals other rivals the price that they would pay for similar assaults.

A second reason why we hypothesize that adaptations for homicide have design features that are unique from adaptations for non-lethal violence is that dead people cannot directly retaliate. A battered, but living rival can recuperate, enlist allies, and seek revenge. By aggressing against, but not killing someone, a person creates new adaptive problems that would not exist if the person was dead, such as the threat of escalating violence from the victim of the aggression, a possible increase in the likelihood of retribution from the kin and social allies of the victim who is able to tell them about the violent incident. The different outcomes of murder and non-lethal violence contributed to different sets of selection pressures for each. We hypothesize that homicide mechanisms will be more likely to activate and lead to actual killings' in situations where the continued existence of an individual after a conflict extends a long shadow of costs into the future that outweigh the costs that will follow from the victim's murder.

Third, a person who intends to use non-lethal violence faces the problem of using an appropriate amount of force to alter conspecifics' behaviors in desired ways, but not kill them. In many contexts, this would not be a problem, depending on the function of the violence. If the violence is to prevent a child from stealing a toy, for example, a low level of violence would suffice, just enough to prevent the child from walking off with one's property. If however, the violence is to convince a rival to stay away from one's wife or daughter, there may be an increased risk that they will die from their wounds. If a person murders another human, whether it is intentional or not, greater costs are typically inflicted on the victims, their kin, and their coalition, on average, than if they had not died (unless the survivors of attempted lethal aggression became significantly burdensome). This introduces a unique problem for individuals who use non-lethal violence with which killers need not concern themselves-they want to inflict injuries that function to influence the behavior of the victim, but are short of murder. Stabbing a victim in the stomach or dropping a large rock on a victim's head, for example, have a non-trivial probability of ending the victim's life. This is not to say that strategies forged by selection to kill must produce instant death. In the ancestral past, without antibiotics or other modern medical treatments, it might take days or weeks for victims of lethal aggression to succumb to infection or other complications of their injuries. Clearly, some behavioral strategies that people have at their disposal to commit murder are not available to those engaging in non-lethal violence. Likewise, some behaviors implemented in strategies of non-lethal violence are not effective means of killing a person. We propose that psychological adaptations that produce non-lethal aggression rely on a set of behavioral strategies that have a very low probability of killing. In contrast, psychological adaptations that produce lethal aggression rely on a different set of strategies that have a high probability of killing.

Fourth, the potential benefits that could flow to a successful killer can be much greater than the benefits that flow to a non-lethal aggressor. Of any competitive strategy, homicide has the highest probability of a zero sum outcome. A dead competitor can no longer control resources, leaving them up for grabs among surviving conspecifics. As a result of the victim's death, more resources become available, on average, than as a result of non-zero sum competitions. We hypothesize that homicide would be particularly favored as a strategy when it frees more resources and when killers perceive a high probability of being able to control and monopolize those resources.

Actual homicides represent the consequence of only a small subset of designed homicidal ideation. Most thoughts of murder do not lead to actual killings. Instead, the majority of people's homicidal fantasies are not acted upon. Most thoughts of killing, we hypothesize, are rejected because the costs of murder are evaluated to be too high and the benefits too low relative to alternative behavioral strategies that have non-lethal outcomes. Indeed, one hypothesized function of homicidal ideation, ironically, is to inhibit a murderous strategy when the costs outweigh the benefits relative to alternative solutions for the relevant adaptive problem. Consequently, only a small percentage of homicidal thoughts become reality.

Just as there are likely differences in the psychological adaptations that lead to murder as the solution to different adaptive problems, there are also likely similarities in the function of many, if not all, homicide mechanisms. What follows is a brief outline of some of the evolved functional components of human murder adaptations for conspecific killing.

10.1. Sensitive to adaptive problems solvable by homicide

One design feature of adaptations for murder is that they should only become activated when an individual faces problems with extremely high fitness consequences ancestrally solvable by killing a conspecific. We hypothesize that such contexts include, threats to the lives of self or kin, the loss of a valuable mate, the loss of valuable territory or resources, and the loss of status and reputation.

10.2. Catalog homicide-relevant information

A second hypothesized design feature of adaptations for murder is the cataloging of homicide-relevant information present in the local environment. Such information includes: specific methods of killing and the location of tools available for murder, the lethality of each method, and the particular reputational consequences of killing in solution to different adaptive problems. Other mechanisms are hypothesized to simultaneously keep track of the particular costs and benefits of each method of killing. This information would be used to calibrate murder adaptations to favor some available murder strategies over others.

10.3. Estimate formidability of victims

One danger of murdering another person is the risk of being physically injured in the process. To address this problem, we hypothesize that selection fashioned mechanisms to factor the physical formidability of the victim into decisions about which among available methods would be most effective at killing the person. Similar mechanisms would also estimate the formidability of the kin and social allies of the intended victim, providing information about the ability to fend off retribution from them and control the resources that may be acquired through killing. Researchers have found that people do spontaneously assess the strength and fighting ability of rivals from looking at their bodies and faces (Sell et al., 2009).

10.4. Forecast likely consequences of murder

The range of outcomes of killing in solution to each adaptive problem is hypothesized to be as recurrent over our evolutionary history as the specific contexts leading to murder. This would have provided selection pressure for mechanisms capable of forecasting the likely future consequences of murder, such as the reputational consequences of the homicide and the probability and type of retribution likely to be pursued by the kin and social allies of the victim.

10.5. Cognitively simulate killing

Symons (1979) argues that sexual fantasies evolved to deal with rare, complex problems. His argument is based on the premise that a function of ideation is to help solve adaptive problems. Even if only a small fraction of sexual fantasies lead to an actual sexual encounter, the fantasies themselves are still functional, low-cost preparations for events with very potentially high fitness consequences. It is the high fitness consequences of sexual behavior that selected for the production of fantasies about sex. Similarly, we argue that the high fitness consequences of homicide selected for specific, directed thoughts of murder.

What constitutes homicidal premeditation in a court of law differs from our conceptualization of the homicidal fantasies that we hypothesize evolved to be functional design features of some homicide adaptations. In a court of law, premeditated murder involves clear evidence of a reasonably extended duration of planning before the killing took place. Premeditated murders are typically viewed by juries and the public as more heinous because the killer had time to evaluate their homicidal fantasy and chose to follow through with it despite recognizing it to be a violation of morality and the law (Hickey, 2003). For homicidal fantasies to be functional in helping to organize the behavior of killers, a short temporal lapse between the experience of the homicidal ideation and the actual killing provides evidence of special design for homicide, even if it appears "impulsive" and would not cross the legal threshold of "premeditation." Protracted deliberative evaluations of the long-term ramifications of the killing, the costs suffered by the victim, morality, or legality need not be part of these fast action homicidal fantasies in order for them to qualify as evolved cognitive design for murder.

We hypothesize that selection would have favored the activation of fast action homicidal fantasies to exploit evolutionarily recurrent situations in which victims were vulnerable or adaptive problems solvable by homicide could be addressed effectively only within narrow windows of time. Indeed, selection may have acted against longer duration fantasies in some circumstances that would have inhibited homicidal action. For example, a man who walks in on his wife in the act of having sex with another man is presented with a brief time frame in which his potential victims are extremely vulnerable to lethal attack. Only a fast action fantasy could take advantage of his victims fleeting vulnerability.

Furthermore, we hypothesize that neither protracted or elaborate fantasies about killing are required in every context in order to effectively produce homicidal behavior. A newborn's anti-homicide defenses that a new mother needs to overcome in order to commit infanticide, for example, are relatively weak. Newborns are helpless to defend themselves and are physiologically fragile. Their deaths can be produced with greater haste, with less planning, and can be more easily blamed on causes other than murder. We hypothesize that the so-called "shaken baby syndrome" is the result of activation of adaptations for infanticide. Parents who shake their babies most often report that they only did it to try to quiet their children down. However, a number of characteristics of the contexts in which shaken baby syndrome is likely to occur are consistent with evolutionary predictors of infanticide, such as: conflict between the parents, blaming the infant for interfering with the parent's romantic relationships, unemployment or financial difficulties, and post partum depression (Lazoritz & Palusci, 2002).

Shaken baby syndrome reliably leads to infant death from traumatic brain injuries (Geddes et al., 2003; Lancon, Haines, & Parent, 1998). The killing of healthy, adult rivals, on the other hand, is relatively more difficult to complete and would benefit from the additional computational power of scenario building. Adults will

actively fight back against a killer. Substantially more force is required to bring about rivals' violent deaths. It is also more difficult to make the violent death of a rival look like something other than a homicide, which may lead the genetic relatives and social allies of a murdered rival to seek revenge on the killer.

A number of problems need to be addressed in order for a cognitive system to support homicidal ideations. First, psychological mechanisms must activate scenario building and focus it on homicide as the solution to an adaptive problem or problems. We hypothesize that homicidal ideations, like actual murders, will be more likely to occur when the elimination of another individual contributes to the solution of numerous adaptive problems simultaneously. The more problems killing solves, the more likely someone will end up dead. Consistent with Symons's (1979) logic about sexual fantasies, thoughts of murder occur in response to rare, complex sets of circumstances for which the devotion of greater cognitive resources is required to evaluate the efficacy of and possibly implement a homicidal strategy.

Once ideation is activated and focused to explore a homicidal strategy, specific content must be provided to move the scenario forward. Not any and all kinds of content would be appropriate for a functional murder fantasy. We hypothesize that mechanisms evolved specifically to direct scenario building for homicide. These mechanisms select and organize the introduction of inputs into homicidal fantasies across time. "Decisions" about what input to introduce and when are based on the ancestral frequency and fitness consequences of similar scenarios. We hypothesize that not one, but many homicidal scenarios may be constructed, guided by psychological mechanisms that organize and reorganize the introduction of inputs over time to explore the range of possible contingencies and outcomes of a plan to kill. In sum, mechanisms are hypothesized to vary the kind of information introduced and the timing of the introduction of specific variables across multiple, distinct incarnations of a plan for murder. Homicide mechanisms are also hypothesized to change the values of the individual variables that are introduced in order to predict the range of likely outcomes of attempting to kill.

We hypothesize that specific mechanisms evolved to forecast the likely future costs and benefits of each specific behavior leading to a homicide. These forecasts are based on two factors: would-be killers' fantasized future representations of themselves and features of the fantasized future environment relevant to a plan for murder. Some features of both are essentially unchanging, such as a person's height and the force of gravity, and would be constants in calculations of the likely outcomes of a homicidal strategy. Other features are more variable. We hypothesize that mechanisms evolved to produce estimates of the values of variable features of the fantasized future representations of self and fantasized future environment in which a strategy of homicide may be adopted.

Each variable feature is likely variable only within a specific range of values, often functionally represented in terms of a normal distribution. For example, the formidability of intended murder victims is likely to vary predictably within a fairly narrow range. Estimates could be based on such factors as their size, age, and observations of their behavior. These estimates are hypothesized to be integrated into calculations of the likely future effectiveness of a particular plan for killing.

10.6. Uncertainty

An important factor hypothesized to increase the complexity of using lethal aggression as part of a strategy to solve adaptive problems is uncertainty. Varying degrees of uncertainty pervade every aspect of adaptive problems solvable by homicide. There is uncertainty about the reliability of the environmental cues that activate adaptations for homicide. For example, is a rival having clandestine sexual encounters with a person's mate or are the two of them just friends who enjoy each other's company? Uncertainty also surrounds the estimates of variables entered into calculations of every aspect of a homicide scenario—from how much physical force a particular weapon will require to end someone's life, to how vigorously the victim will fight back, to how easily the murder could be covered up, to how likely genetic relatives of the victim will be to seek revenge. Seeking out additional information is one strategy to decrease uncertainty. A person can test the strength of social alliances, the lethality of a weapon, or learn the daily routine of an intended victim to discover when they are most vulnerable. Meticulous planning of every detail of a murder informed by additional information may also make killers' minds more certain of the outcome of their plans. Some degree of uncertainty, however, always remains.

As a homicidal strategy actually unfolds over time, some aspects of a situation may occur in ways that were not anticipated. This can happen for at least three reasons. First, incorrect knowledge may be entered into the calculations that underpin plans for murder. Assumptions may be made about the formidability of a victim, for example, based on their size, weight, and observations made of them in limited contexts. If the victim earned a black belt in martial arts years earlier, then this information would be in error and some methods of killing the person likely would be less effective. Second, unanticipated events may confound a plan to kill. For example, a victim may unexpectedly bump into a friend while jogging in the evening, an activity they usually do alone. The presence of their friend may be enough to derail plans for the victim's murder. Finally, killers may fail to enter a relevant piece of information into their homicidal plans. A murder may be planned for night, for example, after the victim is asleep in their house. Killers may not consider how much the darkness would cripple their ability to navigate through their victim's home.

Uncertainty can limit the power of homicide scenario building. As a result, cognitive adaptations for murder must have evolved ways of dealing with the different kinds of uncertainty including abandoning a plan to kill. Errors in plans to kill that stem from problems of uncertainty can derail an attempt at homicide and effectively save a victim's life. In many contexts, we propose that the psychology of would-be killers is not absolutely committed to ending the life of another person rather than doing something else, even if they have a complete plan for murder and have begun implementing that plan. Other intervening factors can redirect a killer's homicidal strategy to non-lethal alternatives at any point in time until their victim is dead.

Clearly, killing people is not the only strategy capable of solving the adaptive problems that can be solved by murder. We propose that mechanisms evolved to weigh the costs and benefits of homicide relative to alternative strategies. The process of creating elaborate homicidal scenarios, of developing a plan to end another person's life, we argue, most often leads people to evaluate that the costs of killing are too high and the benefits too low to actually commit murder.

When the cost of adopting lethal aggression are too great, we hypothesize that evolved mechanisms to inhibit killing steer an individual away from lethal behaviors. Such mechanisms include: emotional charging that makes thoughts or behaviors leading to homicide feel aversive, the diversion of attention to other, non-lethal strategies, and focused scenario-building dedicated to specific nonlethal alternatives. In rare but evolutionarily recurrent instances when a course of action involving conspecific killing is evaluated to be the best among alternative strategies, however, we propose specific evolved mechanisms motivate murder. These mechanisms include: blindness to non-lethal alternatives to homicide, the suspension of empathy or sympathy for the victim, emotional charging capable of producing murderous behaviors, and neurochemical rewards for the exploration and implementation of behaviors capable of killing.

In sum, we propose that the nature of selection pressure forged a number of specific psychological design features that evaluate and infrequently motivate lethal aggression when individuals encounter evolutionarily recurrent contexts that were ancestrally solvable by homicide. These mechanisms are hypothesized to (a) be activated by ancestral conflicts solvable by homicide; (b) store information relevant to lethal aggression for future use; (c) evaluate the formidability of victims, their kin, and allies; and (d) harness the power of scenario building to plan and evaluate the costs and benefits of homicide in the fluid contexts of social life. In the majority of cases, the large costs of homicide are hypothesized to inhibit acting on homicidal urges and steer human behavior in the direction of nonlethal alternatives to killing. Consistent with the logic of coevolutionary arms races between predators and prey of different species, we suggest that evidence of corresponding complexity in the design features of anti-homicide mechanisms to specifically stanch the effectiveness of complex psychological designs that produce homicide provides evidence of adaptation in both. Only Homicide Adaptation Theory has begun to explore the evolutionary history and function of psychological design features that produce conspecific killing.

11. Evidence

Several sources of evidence suggest that mechanisms dedicated to conspecific killing have evolved. These sources of evidence include the following. (For a more complete description of the evidence and explanation of how it applies to Homicide Adaptation Theory, please refer to Buss & Duntley, under review)

 It is more likely that a killer will be someone the victim knows than someone the victim does not know (Buss, 2005). However, Daly and Wilson (1988) have noted that the murder of genetic relatives is significantly less common than the killing of unrelated individuals. Across cultures, 65% of homicides involve males killing other males, 22% involve males killing females, 10% involve females killing males, and only 3% involve females killing other females (Buss & Duntley, under review).

Researchers in the United States found that faster ambulances and better traumatic medical care, much of which was developed during the first Gulf War between the United States and Iraq from 1990 to 1991, have contributed to the decrease in homicide rates during the 1990s in the United States. They estimated that there would be 30,000 to 50,000 additional killings in the United States each year-at least tripling or quadrupling the current homicide rate-without the advances in emergency care technology that have occurred during the last 20 years (Harris, Thomas, Fisher, & Hirsch, 2002). It is reasonable to speculate that modern rates of conspecific killing would be higher still without advances in medical treatments and technology made prior to the first Gulf war.

The homicide rates in many other countries are equivalent to or exceed those in the United States (United Nations, 1998). The lifetime probability of being a homicide victim in Venezuela and Moldova is 1 in 90, twice that of the United States. In Estonia and Puerto Rico, the likelihood is 1 in 60, three times that of the United States. And in Colombia and South Africa, the likelihood is greater than 1 in 20 that a person will die at the hands of a killer, more than ten times the lifetime homicide risk in the United States.

Even among those nations that currently exhibit low homicide rates, much higher frequencies of conspecific killing were a consistent part of their histories. Indeed, the rates of homicide in the distant past of many nations that today enjoy extraordinarily little lethal violence is, from an evolutionary perspective, a quite recent invention (Dower & George, 1995; Eisner, 2003; Ruff, 2001). Additionally, the rates of homicide recorded by nations typically do not include casualties of warfare or genocide.

The homicide rates in industrialized nations pale in comparison to the risk of being killed by a competitor in many preindustrial cultures. Including deaths resulting from lethal raids and tribal warfare, homicides account for roughly one in ten deaths of adult men among the Huli; one in four deaths among the Mae Enga; and one in three deaths among the Dugum Dani and Yanomamo (Chagnon, 1988). Even among the so-called gentle people or peaceful !Kung San of Botswana, there were twenty-two homicides over a twenty-five-year period in a population of 1500, more than four times the rate of killing in a typical year in the United States (Lee, 1984).

2. A large number of species regularly commit conspecific killings in such predictable contexts that it is reasonable to advance the hypothesis that they have adaptations designed to kill. These include the mantis, black widow spiders, jumping spiders, and scorpions (Breene & Sweet, 1985). Males of sexually cannibalistic species (Elgar & Crespi, 1992) use diverse strategies to decrease their chances of being cannibalized: male scorpions sometimes sting the female after deposition of the spermatophore (Polis & Farley, 1979); male black widows (Gould, 1984) and crab spiders (Bristowe, 1958) often restrain females in silk prior to copulation. Conspecific killing, as well as mechanisms to prevent getting killed, appear to be common among insects and arachnids.

Among the 4000 species of mammals, many also have welldocumented patterns of conspecific killing. Male tigers, lions, wolves, hyenas, cougars, and cheetahs have been observed to kill the infants of rival males (Ghiglieri, 1999). These killings often have the effect of hastening the estrus of their mothers, at which point they often mate with the killers. Among primate species, conspecific killings have been well documented among langur monkeys (Hrdy, 1977), chacma baboons (Busse & Hamilton, 1981), red howler monkeys (Crockett & Sekulic, 1984), savanna baboons (Collins, Busse, & Goodall, 1984), mountain gorillas (Fossey, 1984), chimpanzees (Bygott, 1972; Suzuki, 1971), blue monkeys (Butynski, 1982), and others (Hausfater & Hrdy, 1984). The killing of conspecific rival males has also been well-documented among the chimpanzees of Gombe (Wrangham, 1999), as well as in mountain gorillas (Fossey, 1984).

Conspecific killing is widespread, but not universal in the animal world. The circumstances in which many of these conspecific killings occur, such as males killing rivals or the offspring of rivals, provides evidence that some, perhaps many, primate species have evolved adaptations for killing. The cumulative existence pointing to adaptations for within-species killing among primates and other mammals does not imply that such adaptations necessarily exist in humans. But it does suggest that there is no reason to be skeptical about the possibility that adaptations for homicide have evolved in humans.

- 3. Researchers have documented highly patterned distributions of fractures and cranial traumas on ancient human remains that are consistent with death at the hands of another human. They have also discovered arrow tips and stone projectiles lodged in the rib cages and between the vertebrae of ancient humans (Grauer, 1995; Grauer & Stuart-Macadam, 1998; Keeley, 1996 Walker, 1995). These injuries appear predominantly on the left sides of male skeletons, suggesting right-handed attackers (Grauer, 1995; Grauer & Stuart-Macadam, 1998).
- 4. Some ancient tools have several functions, such as hunting and butchering meat. Shock weapons by contrast, such as maces and clubs, serve no function except to inflict injury or death on a human. Keeley (1996) argues that maces, lances, tomahawks, daggers, and swords are excellent for conspecific killing, but have no other apparent purposes.
- The design of fortifications were conceived to defend against attackers and invaders. Castle walls, moats, ditches, drawbridges, and pitfalls have been discovered throughout the world (Keeley, 1996).
- 6. Ancient artists' renderings of conspecific killing appear on rocks and in cave paintings from Europe, the Middle East, and Australia. Ancient Cave paintings discovered in Spain and France show men shooting other men with arrows (Dennen, 1995).

- 7. The cross-cultural and ethnographic record provide extensive documentation of tribal warfare (Keeley, 1996), genocide (Lee, 1984), blood revenge in foraging societies (Daly & Wilson, 1988), intrasexual homicide within groups (Chagnon, 1988; Daly & Wilson, 1988; Hart & Pilling, 1960; Keeley, 1996), infanticide (Daly & Wilson, 1988), and spousal killings (Daly & Wilson, 1988).
- 8. Lethal aggression occurs across cultures in predictable contexts (Daly & Wilson, 1988). For example, female sexual infidelity or defection from a romantic relationship predictably lead to spousal homicide. Conflicts over status and reputation predictably lead to male–male homicide. Deformed or diseased babies, and healthy newborns lacking investing fathers are more likely to be victims of infanticide.

Taken together, the comparative, paleontological, archeological, pictorial, ethnographic, cross-cultural, and contemporary evidence all suggest that homicide has been shaped by evolutionary processes. It is not implausible a priori to hypothesize that humans have evolved psychological mechanisms that are designed specifically for killing other humans in certain contexts. Indeed, these multiple sources of evidence simultaneously provide varying levels of direct and circumstantial support for Homicide Adaptation Theory, including: (a) homicide is a feature of all human societies cross-culturally and historically at rates higher than in contemporary society; (b) intra-specific killing has evolved in other species under certain contexts; and (c) homicide is patterned in clear and consistent ways with males more likely to be both offenders and victims.

12. Limitations and future directions

Many of the hypotheses generated by Homicide Adaptation Theory have yet to be tested. Some lines of argument to address gaps in the logic of the theory, such as how selection pressures unfold over time as homicidal solutions to adaptive problems are enacted, are being developed. Furthermore, we make no claims that Homicide Adaptation Theory can explain all conspecific killings. Some are undoubtedly byproducts of adaptations favored for their non-lethal consequences, as Daly and Wilson (1988) have argued. Some are undoubtedly caused by pathologies or the malfunctioning of psychological adaptations induced by brain damage, genetic abnormalities, or evolutionarily novel influences such as methamphetamine intoxication. Nor do we claim that existing evidence clearly adjudicates between the byproduct hypothesis and Homicide Adaptation Theory. No single piece of evidence may ever be able to do so. However, we suggest that when the overall weight of the evidence is considered, Homicide Adaptation Theory must be viewed as a viable contender for explaining why people kill. Over the next decade, we anticipate that our ongoing cross-cultural research on homicidal fantasies, scenario studies that examine the influence of specific factors on people's willingness to kill, exploration of homicide case files, and studies of anti-homicide defenses will yield additional evidence that will adjudicate among competing theories of homicide.

13. Conclusion

In this article, we have outlined Homicide Adaptation Theory and its fundamental logic. We discussed examples of the unique selection pressures created by human cognitive adaptations for social exchange that are hypothesized to have selected for homicide. We articulated the theory of a co-evolutionary arms race between adaptations for homicide and defenses against being killed. We explored several of the hypothesized design features of psychological adaptations for homicide. Finally, we briefly examined some of the range of evidence that can be brought to bear in evaluating the theory. There is much work to be done before we have a complete understanding of the causes of homicide. Despite its current conceptual and evidentiary incompleteness, and despite the possible intuitive repugnance people have about the possibility that humans have adaptations to kill, we suggest that Homicide Adaptation Theory offers the promise of providing new causal insights into murder previously undiscovered and unexplained by prior theories of homicide.

References

- Breene, R. G., & Sweet, M. H. (1985). Evidence of insemination of multiple females by the male black widow spider, Latrt, dectus maclans [I'Araneae, Theridiidae]. Journal of Arachnology, 13, 331–336.
- Bristowe, W. S. (1958). The world of spiders. London: Collins.
- Buss, D. M. (2000). The dangerous passion: Why jealousy is as necessary as love and sex. New York: Free Press.
- Buss, D. M. (2003). The evolution of desire (rev. ed.). New York: Free Press.
- Buss, D. M. (2005). The murderer next door: Why the mind is designed to kill. New York: The Penguin Press.
- Buss, D.M., & Duntley, J.D (1998). Evolved homicide modules. Paper presented to the Annual Meeting of the Human Behavior and Evolution Society, Davis, California, July 10.
- Buss, D.M., & Duntley, J.D. (1999). Killer psychology. Paper presented to the Annual Meeting of the Human Behavior and Evolution Society, Salt Lake City, Utah.
- Buss, D. M., & Duntley, J. D. (2003). Homicide: An evolutionary perspective and implications for public policy. In N. Dess (Ed.), Violence and public policy (pp. 115–128). Westport, CT: Greenwood Publishing Group, Inc.
- Buss, D. M., & Duntley, J. D. (2006). The evolution of aggression. In M. Schaller, J. A. Simpson, & D. T. Kenrick (Eds.), *Evolution and social psychology* (pp. 263–286). New York: Psychology Press.
- Buss. D. M., & Duntley. J. D. (under review). Homicide adaptation theory.
- Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., & Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *The American Psychologist*, 53, 533–548.
- Buss, D. M., Larsen, R. R., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. Psychological Science, 3, 251–255.
- Buss, D. M., & Schmitt, D. P. (2011). Evolutionary psychology and feminism. Sex Roles, xx xxx-xxx.
- Busse, C., & Hamilton, W. J., III (1981). Infant carrying by adult male chacma baboons. Science, 212, 1281–1283.
- Butynski, T. M. (1982). Harem male replacement and infanticide in the blue monkey (Cercopithecus mitis Stuhlmann) in the Kibale Forest, Uganda. American Journal of Primatology, 3, 1–22.
- Bygott, J. D. (1972). Cannibalism among wild chimpanzees. *Nature*, 238, 410–411.
- Campbell, A. (1999). Staying alive: Evolution, culture and women's intra-sexual
- aggression. The Behavioral and Brain Sciences, 22, 203–252. Chagnon, N. (1988). Life histories, blood revenge, and warfare in a tribal population. Science, 239, 985–992.
- Collins, D. A., Busse, C. D., & Goodall, J. (1984). Infanticide in two populations of savanna baboons. In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparative and* evolutionary perspectives (pp. 193–216). New York: Aldine.
- Crabb, P. B. (2000). The material culture of homicidal fantasies. Aggressive Behavior, 26, 225–234.
- Crockett, C. M., & Sekulic, R. (1984). Infanticide in red howler monkeys. In G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp. 173–192). New York: Aldine.
- Daly, M., & Wilson, M. (1988). Homicide. Hawthorne, NY: Aldine.
- Daly, M., & Wilson, M. (1989). Homicide and cultural evolution. *Ethology and Sociobiology*, 10, 99–110.
- Daly, M., & Wilson, M. (1998). The evolutionary social psychology of family violence. In C. Crawford & D. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues and applications* (pp. 431–456). Mahwah NJ: Erlbaum.
- Daly, M., & Wilson, M. (1999). An evolutionary psychological perspective on homicide. In M. D. Smith & M. A. Zahn (Eds.), *Homicide: A sourcebook of social research* (pp. 58–71). Thousand Oaks: Sage Publications.
- Dennen, J. M. G. V. D. (1995). The origin of war. Groningen, The Netherlands: Orion Press.
- Dobash, R. E., Dobash, R. P., Cavanagh, K., & Medina-Ariza, J. (2007). Lethal and nonlethal violence against an intimate female partner: Comparing male murderers with non-lethal abusers. *Violence Against Women*, 13, 329–353.
- Dodge, K. A., Bates, J. E., & Pettit, G. S. (1990). Mechanisms in the cycle of violence. Science, 250, 1678–1683.
- Dower, J. W., & George, T. S. (1995). Japanese history and culture from ancient to modern times. Princeton. NJ: Markus Wiener.
- Duntley, J. D. (2005). Adaptations to dangers from other humans. In D. Buss (Ed.), The handbook of evolutionary psychology (pp. 224–249). New York: Wiley.
- Duntley, J. D., & Buss, D. M. (1998). Evolved anti-homicide modules. Davis, CA: Paper presented to the Annual Meeting of the Human Behavior and Evolution Society.
- Duntley, J. D., & Buss, D. M. (1999). Killer psychology: The evolution of mate homicide. Salt Lake City, UT: Paper presented to the Annual Meeting of the Human Behavior and Evolution Society.
- Duntley, J. D., & Buss, D. M. (2000). The killers among us: A co-evolutionary theory of homicide. Amherst, MA: Invited paper presented at a special symposium organized by the Society for Evolution and the Law at the Annual Meeting of the Human Behavior and Evolution Society.

- Duntley, J. D., & Buss, D. M. (2001). Anti-homicide design: Adaptations to prevent homicide victimization. London: Paper presented to the Annual Meeting of the Human Behavior and Evolution Society.
- Duntley, J. D., & Buss, D. M. (2002). Homicide by design: On the plausibility of psychological adaptations for homicide. Invited presentation for the First Annual AHRB Conference on Innateness and the Structure of the Mind: University of Sheffield, England.
- Duntley, J. D., & Buss, D. M. (2005). The plausibility of adaptations for homicide. In P. Carruthers, S. Laurence, & S. Stich (Eds.), *The structure of the innate mind* (pp. 291–304). New York: Oxford University Press.
- Duntley, J. D., & Buss, D. M. (2008). The origins of homicide. In J. Duntley & T. Shackelford (Eds.), Evolutionary forensic psychology (pp. 41–64). New York: Oxford University Press.
- Eibl-Eibesfeldt, I. (1989). Human ethology. New York: Aldine de Gruyter.
- Eisner, M. (2003). Long-term historical trends in violent crime. *Crime and Justice*, 30, 83–142. Ellison, P. T. (1985). Lineal inheritance and lineal extinction. *Behavioral and Brain Sciences*. 8, 672.
- Cannibalism: Ecology and evolution among diverse taxa. Elgar, M., & Crespi, B. J. (Eds.). (1992), Oxford, U.K: Oxford University Press.
- Federal Bureau of Investigation (2010). Expanded homicide data. Retrieved 19 October 2010 from. http://www2.fbi.gov/ucr/cius2009/offenses/expanded_information/homicide.html
- Fossey, D. (1984). Gorillas in the mist. Boston: Houghton Mifflin.
- Gartner, R. (1990). The victims of homicide: A temporal and cross-national review. *American Sociological Review*, 55, 92–106.
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, 126, 55–77.
- Geddes, J. F., Tasker, R. C., Hackshaw, A. K., Nickols, C. D., Adams, G. G., Whitwell, H. L., et al. (2003). Dural hemorrhage in non-traumatic infant deaths: Does it explain the bleeding in 'shaken baby syndrome'? *Neuropathology and Applied Neurobiology*, 29, 14–22.
- Ghiglieri, M. P. (1999). The dark side of man: Tracing the origins of violence. Reading, MA: Perseus Books.
- Glenn, A. L., Kurzban, R., & RAine, A. (in press). Evolutionary theory and psychopathy. Aggression and Violent Behavior.
- Gould, S. J. (1984). Only his wings remained. Natural History, 93, 10-18.
- Gould, S. J. (1991). Exaptation: A crucial tool for evolutionary analysis. Journal of Social Issues, 47, 43–65.
- Grauer, A. L. (1995). Bodies of evidence: Reconstructing history through skeletal analysis. New York: Wiley-Liss.
- Grauer, A. L., & Stuart-Macadam, P. (Eds.) (1998). Sex and gender in paleopathological perspective. New York, NY: Cambridge University Press.
- Haig, D. (1993). Genetic conflicts in human pregnancy. The Quarterly Review of Biology, 4, 495–532.
- Harris, A. R., Thomas, S. H., Fisher, G. A., & Hirsch, D. J. (2002). Murder and medicine. Homicide Studies, 6, 128–166.
- Hart, C. W., & Pilling, A. R. (1960). The Tiwi of North Australia. New York: Hart, Rinehart, & Winston.
- Hausfater, G., & Hrdy, S. B. (Eds.). (1984). Infanticide: Comparative and evolutionary perspectives. New York: Aldine.
- Hickey, E. (2003). Encyclopedia of murder and violent crime. Thousand Oaks, CA: Sage. Hrdy, S. B. (1977). Infanticide as a primitive reproductive strategy. Americian Scientist, 65, 40–49.
- Holland, B., & Rice, W. R. (1998). Chase-away sexual selection: Antagonistic seduction versus resistance. Evolution, 52, 1–7.
- Kaplan, H. S., & Gangestad, S. W. (2005). Life history theory and evolutionary psychology. In D. M. Buss (Ed.), *Handbook of evolutionary psychology* (pp. 68–95). New York: Wiley.
- Keeley, L. H. (1996). War before civilization. New York: Oxford University Press.
- Kenrick, D. T., & Sheets, V. (1993). Homicidal fantasies. Ethology and Sociobiology, 14, 231–246.
- Kruger, D. J., & Nesse, R. M. (2004). Sexual selection and the Male:Female Mortality Ratio. Evolutionary Psychology, 2, 66–85.
- Lalumière, M. L., Mishra, S., & Harris, G. T. (2008). In cold blood: The evolution of psychopathy. In J. Duntley & T. K. Shackelford (Eds.), Evolutionary forensic psychology: Darwinian foundations of crime and law (pp. 139–159). New York: Oxford University Press.
- Lancon, J., Haines, D., & Parent, A. (1998). Anatomy of the shaken baby syndrome. Anatomical Record, 253, 13–18.
- Lazoritz, S., & Palusci, V. J. (2002). Shaken baby syndrome: A multidisciplinary approach. Binghamton, NY: Haworth Press.
- Lee, R. B. (1984). The Dobe !Kung. New York: Holt. Rinehart and Winston.
- Marshall, I. H., & Block, C. R. (2004). Maximizing the availability of cross-national data on homicide. *Homicide Studies*, 8, 267–310.
- Mealey, L. (1995). The sociobiology of sociopathy: An integrated evolutionary model. *The Behavioral and Brain Sciences*, 18, 523–599.
- Nesse, R. M., & Williams, G. C. (1994). Why we get sick. New York: Times Books Random House.
- Niehoff, D. (1999). The biology of violence. New York: Free Press.
- Pitchford, I. (2001). The origins of violence: Is psychopathy an adaptation? The Human Nature Review, 1, 28–36.
- Polis, G. A., & Farley, R. D. (1979). Behavior and ecology of mating in the cannibalistic scorpion *Paruroctonus mesaensis* Stahnke (Scorpionida: Vaejovidae). *Journal of Arachnology*, 7, 33–46.
- Rhee, S. H., & Waldman, I. D. (2002). Genetic and environmental influences on antisocial behavior: A meta-analysis of twin and adoption studies. *Psychological Bulletin*, 128, 490–529.

Ruff, J. R. (2001). Violence in early modern Europe 1500–1800. Boston: Cambridge University Press.

- Saraiya, M., Green, C. A., Berg, C. J., Hopkins, F. W., Koonin, L. M., & Atrash, H. K. (1999). Spontaneous abortion-related deaths among women in the United States – 1981–1991. Obstetrics and Gynecology, 94, 172–176.
- Schmitt, D. P., Shackelford, T. K., Duntely, J., Tooke, W., & Buss, D. M. (2001). The desire for sexual variety as a key to understanding basic human mating strategies. *Personal Relationships*, 8, 425–455.
- Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society B*, 276, 575–584.
- Suzuki, A. (1971). Carnivority and cannibalism observed in forest-living chimpanzees. Journal of the Anthropological Society of Nippon, 74, 30–48.
- Symons, D. (1979). The evolution of human sexuality. New York: Oxford University Press.
- Tooby, J. & Cosmides, L. (1988). The evolution of war and its cognitive foundations. Institute for Evolutionary Studies, Technical Report #88-1.
- Tooby, J., & Cosmides, L. (2010). Groups in mind: The coalitional roots of war and morality. In Høgh-Olesen Henrik (Ed.), Human morality & sociality: Evolutionary & comparative perspectives. New York: Palgrave MacMillan.

- Trinkaus, E., & Shipman, P. (1993). *The Neanderthals: Changing the image of mankind.* New York: Alfred A. Knopf.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), Sexual selection and the descent of man: 1871–1971 (pp. 136–179). Chicago: Aldine. United Nations (1998). United Nations 1996 Demographic Yearbook. New York: Author.
- Walker, P. (1995). Documenting patterns of violence in earlier societies: The problems and promise of using bioarchaeological data for testing evolutionary theories. Santa Barbara, CA: Paper presented at the Annual Conference of the Human Evolution and Behavior Society.
- Werner-Wilson, R. J. (1998). Gender differences in adolescent sexual attitudes: The influence of.
- Wilson, M., & Daly, M. (1985). Competitiveness, risk-taking, and violence: The young male syndrome. *Ethology and Sociobiology*, 6, 59–73.
- Wilson, M., Daly, M., & Daniele, A. (1995). Familicide: The killing of spouse and children. Aggressive Behavior, 21, 275–291.
- World Bank (2009). World development indicators. Retrieved 19 October 2010 from. http://data.worldbank.org/data-catalog/world-development-indicators? cid=GPD_WDI
- Wrangham, R. (1999). Evolution of coalitionary killing. Yearbook of Physical Anthropology, 42, 1–30.