

AN EVOLUTIONARY PERSPECTIVE ON WAR

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*Four things greater than all things are, —  
Women and Horses and Power and War.*

-Rudyard Kipling

Conflict is as old as life. In fact, if evolutionary and behavioral ecological theory are correct, conflicts of interest, if not open aggression, are universal among living things. While some authors (e.g. Ferrill 1985) suggest that the origins of war are simply prehistoric, an evolutionary or behavioral ecologist would argue that by any functional definition, war — lethal conflict — is older than humanity itself. From an evolutionary perspective, two considerations have profound consequences: the reproductive impacts for individuals of fighting and killing (including formal war), and the potential conflicts of interest among different individuals involved in conflict. To examine the evolution of war, I will begin not with complex and formal international military conflicts, but with much simpler conflict in non-human species, asking: Over evolutionary time, what has been the ecological context of conflict and killing in hominids and other mammals? Under what ecological circumstances are these likely to occur, and what are the costs and benefits to the individuals involved? The functional nature of conflict may become clearer in these simpler cases; then more complex cases may be amenable to approach.

### **The Natural Selection Paradigm**

The organisms we see today are the descendants of those that most successfully survived and reproduced in past environments; it is only half a joke that the one thing we can say with assurance is that none of our ancestors were sterile. Strategies for survival and reproduction are all-important, though their appropriate analysis may be complicated. At its simplest, the analytic background derives from the differential survival and reproduction of individuals which use various strategies. This simple logic, first explicitly employed by Darwin (1859), gives rise to complex and profound effects. Even for relatively non-social animals, success is seldom achieved by the strategy "eat and reproduce all you can as quickly as you can." Successful reproduction does not necessarily involve producing the most offspring, or even the most surviving offspring.

Risky strategies like physical conflict seem at first likely to be selected against. In fact, Darwin treated such risky behaviors separately from natural selection, as sexual selection, because he was unable to see how risking one's neck could be reproductively advantageous. Yet as we will see, it can. Another non-obvious outcome of the action of selection is that co-operation can be an intensely competitive strategy. Reciprocity is common among individuals who spend time together, interacting repeatedly, rather than among strangers. When risks are high for behavior benefiting others, such behaviors are likely to occur only or primarily among kin. That is, if my potential cost

for helping you is high, I am likely to defect unless you are a close relative (in which case, my genes may be assisted even if I die). In the evolution of warfare, this fact becomes central. Even among kin, of course, blind altruism is not predicted (e.g., Alexander 1979, 1987). Individuals have an array of variously-related individuals with whom to interact, and far from becoming blind altruists within their group, humans have become complex social strategists — judging costs and benefits, current and future, and behaving reciprocally as well as nepotistically (Alexander 1987, Humphrey 1983). Thus, for example, we see the use of kinship terms as a proximate device to promote xenophobia. Such manipulations of kinship terms (e.g., Johnson 1986, Johnson et al. 1987, Chagnon 1982), are important, but are unlikely to create and drive major conflicts consistently in the absence of strong selective advantages to major actors in the conflict.

Lethal conflict, as a phenomenon, is like delayed reproduction, kin selection, direct and indirect reciprocity; all are phenomena that at first glance look as though they should decrease, rather than increase, reproduction — but in fact, each is found in specific, ecologically predictable, circumstances (e.g. see Cronk 1991, Daly and Wilson 1983, 1988). In those environments, their impact is increased net reproductive success, measured as inclusive fitness (Hamilton 1964). Were this not true, these behaviors would remain rare.<sup>1</sup>

As in any behavioral analysis, it is important to distinguish **proximate cues**, or triggers, for behaviors from **ultimate adaptive** causes. If we ask, for example, why a bird migrates, one answer might be "changing day length causes hormonal changes, triggering migration." This answer elucidates the proximate cue, but does not explain why individuals in some species but not others migrate, why, within species, some individuals migrate, and not others, and why daylength (as opposed to temperature, some other cue, or a combination of cues) has become the cue. The ultimate cause of migration is a seasonal better-versus-worse shift in (for example) foraging and nesting areas; individuals who follow the better areas, shifting seasonally, leave more descendants than those who remain in one area. When daylength is a reliable predictor of these seasonal shifts, individuals who use it as a cue will fare better than those using some other proximate cue or failing to leave as the environment deteriorates. The benefits and costs of migration may differ substantially for older, prime-age birds, compared to yearlings; in such cases, different categories of individuals are more or less likely to migrate.

Even in a simple example like migration, it should be clear that this is a behavioral ecological argument, based on the relative reproductive costs and benefits of individuals, and does not require that a specific "gene for migration" be postulated. Similarly, we do not postulate some sort of "gene" for warfare; rather we ask under what environmental conditions warfare arises, who does it, and who benefits reproductively. Even in simple behaviors, selection has frequently operated on complexes of loci, many of which affect other behaviors, and which influence some part of the response system. External environment, development, and genes interact in a complex way. Just as

many different environmental cues can be proximate cues triggering migration (whatever is the most reliable, predictable co-variant with environmental quality is the trigger predicted), so can many different internal mechanisms be called upon to create complexes of behavior, including conflict behavior. While for many important behaviors we cannot specify genetic loci involved (see Graf en 1984), we study trait-environment correlations, and can often make powerful and unexpected predictions from these, using selection theory (see Cronk 1991).

A final complication, extremely important in the case of lethal conflict, is that of evolutionary novelty. Imagine a reproductively advantageous behavior; if ecological conditions change, there is a possibility for that behavior to be driven by proximate cues (which in the past correlated with reproductive advantage), even when the proximate cues are currently unhinged from the (past) functional advantage. This is most common when environmental changes represent evolutionarily novel events, such as human technological changes.

Sugar is a simple example of an evolutionary novelty. For omnivores, sampling new foods represents a risk. It is common in many species both to sample new foods at a low level and to use correlates in establishing preferences; if there are toxic effects, they will be likely to be minimal and simply unpleasant rather than lethal. Sweet foods are seldom harmful, and sour and bitter tastes are often correlated with the presence of harmful alkaloids. So a preference for sweet tastes has become widespread in omnivores. In natural situations, it is difficult to obtain sufficient sugar without other nutrients and fiber to create problems of obesity. Once we invented technologies for refining and concentrating sugar, we created foods that had enormous concentrations of sugar. Now the selective link had been broken between sweet taste (the proximate cue) and good food source (resulting in enhanced nutritional status). But there is no evidence that organisms evolve to have any awareness of ultimate selective relationships — proximate cues drive the system, and natural selection operates as a passive sieve through differential survival and reproduction. So, we retain a preference for sweet taste that is often currently counter-adaptive (including health risks like obesity and dental caries, and perhaps sexual selection).

In the case of lethal conflict, we must examine not only whether it has ever created a selective advantage for those individuals engaging in it, and whether there is any current utility, but also, whether, as the character and scope of war have changed, any previous advantage has been disconnected from the proximate cues that have driven the conflict (comradeship, exhilaration in risky situations, pride in achievement, etc). Thus, we need to ask: [1] was there previously reproductive advantage to engaging in lethal conflict; [2] is there currently reproductive advantage to engaging in lethal conflict; and [3] are the proximate triggers to conflict "unhooked" from any previous selective advantage?

## **Resources and Conflict: Predictions from Selection Theory**

The argument above suggests that conflict is likely to center on items of real reproductive importance: mates, or status and resources when these contribute to reproductive success. Particularly when significant risks are involved, conflict over resources of little value is unlikely.

In non-human species, damaging aggression is surprisingly widespread. Typically, it arises from fights over mates or resources for getting mates, from infanticide, and from cannibalism (e.g. Huntingford and Turner 1987). The cost to an infanticidal killer (often a male taking over a harem and killing the offspring of his reproductive predecessor) is likely to be small, and infanticide is more common than the killing of adults. Lethal fighting among individuals of similar age and status can be significant. In red deer, male mortality from sexual competition can approach 13-29% of all adult male mortality (Clutton-Brock et al. 1982). In non-human species, the resource over which conflict occurs is either a direct reproductive resource (territory, mates, etc.), or an indirect reproductive resource (elimination of competitors or competitors' offspring).

The ultimate costs and benefits are reproductive. Parker (1974, 1984) and Maynard Smith and Parker (1976) have used a game-theoretic approach to analyze adversarial relations. Combatants, they argue, assess each other's resource-holding power, and (Parker 1974):

the stake played for is infliction of loss of resource-holding power, and is determined by the fitness budgets of the opponents . . . This defines a critical probability of winning . . . for each combatant, above which escalation (fighting) is the favorable strategy . . . and below which withdrawal is favorable.

Escalation, then, should occur only when the absolute probability of winning minus the critical probability of winning is positive for each combatant. Someone will always lose; if information were perfect, the loser-to-be would never attack, and would always withdraw if attacked. Depending on the costs, the stronger combatant may be expected to press an attack. Displays in many species involve deception and advertisements that make each potential participant appear bigger and stronger — advertising that an attack might prove costly (see also review by Huntingford and Turner 1987).

Open conflict in many species occurs primarily between individuals of the same population, rather than between groups from different populations; such individual conflict is unlikely unless the actors are similar in status or power (e.g. Parker 1974). In red deer, for example, subordinate stags are unlikely to escalate a confrontation — the risks of serious injury are too high. For an already dominant stag, escalation may incur cost for no additional gain. In some primate species, groups of varying size may separate from the main population on foraging trips. If they encounter smaller groups or lone individuals, groups may attack, exploiting the uneven balance of power

(Manson and Wrangham 1991). Such group aggression is not qualitatively different (the context, benefits and costs are similar), but is more complex, with co-operation among individuals.

Evolutionary theory predicts that potentially lethal conflict will occur when the possible reproductive (usually mating, not parental) rewards (mates, status, resources for mates) are high; and that, within mammals, males will more often be in a position to gain than females (next section; also Manson and Wrangham 1991, Alexander 1987, Low 1992). Sexual selection (in competition over mates) and kin selection (in infanticide and inter-group conflicts) will be the driving forces. Inter-group, rather than inter-individual, conflict will occur only in long-lived, social species. Several recent analyses reflect these predictions. Shaw (1985) and Shaw and Wong (1989) have argued that evolutionary explanations may be useful in analyzing warfare in complex nation-states. They focused primarily on kin selection arguments as the background for xenophobia and ethnocentrism, major factors in promoting war (see also Johnson 1986 on the use of kinship terms by political leaders). Kin selection leads to the development of cohesive groups that are predisposed to intergroup conflict (though it does not predict the sex differences we see in most mammals). Ethnicity is the remnant of this process in modern societies. Kinship ties, as noted above, change the costs and benefits for individuals taking risks in potentially lethal combat.

### Sexual Dimorphism: Why Women Warriors Are Rare

Mammalian aggression is sexually dimorphic. An analysis of coalitions in non-humans makes clear that, compared to females, males tend to form coalitions that are riskier, more aggressive, and more often among non-relatives (Low 1990a,1992, below). Because females' conflicts center on food or parental resources, while males' conflicts are likely to center on the acquisition of mates, the reproductive impact of conflict for male mammals may be many times greater than that for females (Low 1990a).

The return curve for reproductive success gained per unit of resources or status acquired differs for mating and parental effort. Mating effort, typical of mammalian males, has a large fixed cost; then the curve may rise steeply, for additional matings cost relatively little. For example, a red deer male, even to try for a first mating, must grow large (involving a cost of delayed maturation), grow antlers, and fight for dominance and control of good feeding grounds. The initial cost is great; the cost associated with each individual mating is small. For mammalian mothers, each offspring costs approximately as much parental effort as any other, and the maximum possible number of offspring is likely to be lower than for males.

Males, while having the same average number of offspring as females, typically experience more variance in reproductive performance; more males than females in each generation fail to have any offspring in their lives, and the most successful males may have ten times as many offspring in

their lives as the most successful female. Because males' variance is high, the stakes are higher. Great expenditure and risk may be profitable, so risky behavior and conflict are, in polygynous species, male endeavors. Thus sexual conflicts (more frequently male in mammals) seem more likely to escalate to lethal proportions than conflicts arising from other sorts of individual selection.

In humans, too, male reproductive variance exceeds female variance (see Low 1990a); thus it is not surprising that aggression is one of the most consistent sex differences across cultures (Ember 1981, Barry et al. 1976, Low 1989a), and homicides are principally a male endeavor (Daly and Wilson 1988). This difference in risks and returns, of course, is what prompted Darwin (1872) to treat sexual selection differently from "ordinary" natural selection, even though functionally it is identical. Ross's (1983) observation that women's politics and conflict over resources tend to be at the familial and neighborhood level, while men's conflicts tend to have broader scope, is therefore hardly surprising (Low 1990a, 1992); similarly, women warriors are predicted to be rare.

Women warriors, however, are not unknown. During the seventeenth, eighteenth, and nineteenth centuries women occasionally passed themselves off as men and fought in the ranks of infantry and cavalry regiments (Holmes 1875:102). From at least the time of Alexander (Keegan 1987), women travelled and sometimes fought with their men; children were legitimized in Alexander's time after the soldier completed his duties.

Cross-culturally, men can make enormous direct reproductive gains with access to power, status, and great amounts of resources, but it is not clear to what extent women can do so (Low 1990a, 1992); this parallels the reproductive ecology of resource control and status in other polygynous species. In the few societies in which women wield substantial public power, as opposed to informal influence, they evidence no clear reproductive gain. In fact, in some of the examples, it is apparent that there is a conflict between political and direct reproductive gain for women. In matrilineal and double descent systems, women's power appears to accrue to their sons, who may reap reproductive benefit (e.g. Trivers 1985, Clutton-Brock et al 1986, Low 1992). Through evolutionary history, men have been able to gain reproductively by warring behavior; women almost never have been able to do so.

It is important to distinguish this argument from others that might seem similar. This argument does not hinge on sexual size dimorphism in humans — the fact that men are generally bigger and stronger than women. Even in ungulate species like red deer, in which status and resource control are mediated through physical combat, and there is no evidence of reciprocal "political" alliances, size is not the only determinant of status (e.g. Clutton-Brock et al 1982). In primate species, and in human societies, the social complexities so far outweigh the impact of physical size that size alone is a poor predictor of success. Similarly, this argument does not reduce to an assertion that women are bound by the constraints of pregnancy, nursing and child care. If

that were true, sterile women and post-menopausal women might broadly be expected to engage in intergroup conflict, as do other primate females.

Sexual dimorphism in use of resources and power in reproduction is the critical factor. Men appear to seek direct reproductive gain (wives, owed reciprocity) in intergroup conflict, while women, when they are (rarely) involved, seek resources for themselves and their offspring. Sometimes this is accomplished through indirect or informal influence and nepotistic gain. Most commonly, the amount of resources controlled by women is sufficient to support their family, but sometimes, particularly in matrilineal and duolineal societies (Low 1992), women may gain for their families. These societies, like the Cherokee and perhaps the Ashanti, are also those in which there is an occasional woman warrior.

Women have evolved to use resources differently from men in reproductive matters (Low 1990a, 1992), and this has had impact on their involvement in war. Further, patriliney fosters men's, but not women's confluences of reproductive interests in war, because related men — but not women — live together. Adams (1983) pointed out that under these conditions, women face a conflict of interest with their husbands (their husbands may be making war upon their fathers and brothers), and argued that the formal exclusion of women from warfare in so many societies may have its roots here.

Today, it may be true that women in western societies have comparatively great overt economic and political power, but it is also likely that for both men and women, the exercise of formal power may well have less impact on reproduction than in smaller societies. Men may, perhaps, still reap reproductive advantage from open conflict as well as other forms of striving, compared to women, through remarriage and children born to mistresses, but there are few data to allow us to test whether this is true (see Low 1991 for review).

#### War as Runaway Sexual Selection

Human war can become more complex and varied than intergroup aggression in other species, largely as a result of the development of technology (which itself is probably a product of intelligence, and probably a product specifically of Machiavellian intelligence; cf. Alexander 1971, Humphrey 1976, 1983, Byrne and Whiten 1988). The role of sexual selection in lethal conflict and the development of technology to currently lethal levels raise an important question: is war an example of runaway sexual selection, described by Fisher (1958)?

Fisher noted that "remarkable consequences" follow if females exert a strong preference for particular traits in males. As Fisher pointed out, in sexual selection, two influences are important: initial, sometimes considerable, advantages not due to female preference (e.g. the advantage of large antlers in combat for red deer); and any additional advantage conferred by any female preference.



The intensity of preference itself will continue to increase through sexual selection, so long as the sons of females exerting the preference have any advantage over other males. Fisher (1958:152) noted: "The importance of this situation lies in the fact that the further development [of the favored trait] will still proceed, by reason of the advantage gained in sexual selection, even after it has passed the point in development at which its advantage in Natural Selection has ceased."

Thus, the immediate reproductive gains can be so great, and so powerfully selected for, that they outstrip the countering pressure of ordinary natural selection for survival, resulting in the development of lethal traits leading to extinction. When, as in the Yanomamø, warring skill results in a significant increase in the number of children produced (Chagnon 1988), sexual selection can be very powerful. Even in modern industrialized societies, in which participation in wars, and risk-taking behaviors may be "unhooked" from the advantages given by sexual preference, if sexual preference still exists for "war heroes" or if there are other proximate rewards, previously linked to selective advantage, the behavior may still be common.

### Other Biological Approaches to Understanding War

One of the earliest and most influential biological approaches to understanding war was Konrad Lorenz's (1966) *On Aggression*. Lorenz argued that aggression is an instinctive drive favored by selection. Although he specified that this did not make warfare unavoidable, others have inferred some sort of genetic basis (rather than a flexible response to ecological conditions, in which genetically identical individuals might act differently, depending on circumstances). Lorenz also argued that because humans lack lethal weapons in their simple physical makeup, relying on tools, humans also failed to evolve reliable inhibitions against killing each other. Variations of this argument are found in Eibl-Eibesfeldt (1979) and Ardrey (1966). The difficulty with such arguments is that they predict neither the occurrence of aggressive behavior — what conditions (e.g. reproductively important conflicts of interest) are most likely to precipitate aggression — nor the constraints (e.g., individual costs and benefits).

Perhaps in response to just such arguments, well-known and well-respected scientists, in a statement (16 May 1986) for the International Society for Research on Aggression, argued from the fact that there is no evidence for a specific allele for aggression to an argument that warfare was "biologically possible, but... not inevitable, as evidenced by its variation in occurrence and nature over time and space." This view moves from patently true statements (e.g. about the non-evidence of any special alleles for "warring behavior"), to generalizations that "biology does not condemn humanity to war, and that humanity can be freed from the bondage of biological pessimism and empowered with confidence . . . Just as 'wars begin in the minds of men,' peace also begins in our minds . . . The responsibility lies with each of us." Such an approach is hopeful but fails to come

to grips with the ecology of war, the circumstances in which aggression profits the individual or lineage genetically. It remains insufficiently specific or predictive.

Tooby and Cosmides (1988) argued that humans and chimpanzees have particular "Darwinian algorithms" which govern coalition formation, and predispose both species to warfare. They argue that the psychologically imposed structure has certain characteristics: cheaters must be identified and excluded or punished; participants are rewarded or punished in proportion to the risks they take, and in proportion to their contribution to success. Each coalition member has impact on the coalition by regulating his own participation in the coalition and by the actions he takes to enforce the contract on other members. However, all that they specify seems likely to be true for numerous other coalitions (hunting, female lion parental etc; see Low 1990a), and their argument thus does not lead to the deduction that humans and chimpanzees are unique in having the appropriate algorithms for warfare. Further, although Tooby and Cosmides discuss allocation of rewards to participants (that they may be unequal) they fail to address the fact that these payoffs must be compared to payoffs from other strategies (e.g. the dilemma of disenfranchised males). It is important to note, also, that Tooby and Cosmides<sup>1</sup> argument is not a true alternative to the argument I present here: that lethal conflict exists because individuals and families have profited from assuming the risks of lethal conflict under specific conditions, over evolutionary time. There is an argument of proximate psychological mechanism, and mine is a behavioral ecological argument about ultimate causality; both may be true.

Ember and Ember (in press), in a major study of warfare cross-culturally, found some interesting ecological correlations with warfare. The Embers' study is an important contribution to the ecology of war, not an alternative hypothesis to a behavioral ecological one; both may be true. Ember and Ember found that societies went to war when particular sorts of resources became (or threatened to become) limiting. A major predictor was the threat of weather or pest disasters. Given the difficulty of getting really sensitive measures on such a broad scale, their results are strong. Ember and Ember also found that societies with more warfare also encourage boys to be more aggressive, tougher, and show more fortitude. This is consistent with the impact of sexual selection on warfare; Low (1989a) found that the greater the potential reproductive rewards for sons (the greater the degree of polygyny in unstratified societies), the more boys were taught to strive.

As we learn more about behavior, the importance of genes alone pales, particularly for complex conflict. Moore (1991) infers some sort of "warfare allele." If humans have evolved as complex social strategists, as Alexander and Humphrey argue, such an explanation is extremely unlikely. Dawkins (1986:296 et seq.) gives a useful analogy. Genetic coding is like a cake recipe, and in trying to decipher exactly how the cake (the phenotype, the individual) comes to be, it is a hopeless task to try and map any particular crumb of the cake, or any particular trait in the phenotype, to a particular word in the recipe. Thus, changing "350 degrees" to "450 degrees"

changes many things subtly in concert. Perhaps there are a few exceptions: if I change "pecans" to "walnuts" I might find a match - but such cases are very rare.

Lethal aggression is most likely to be a function of the costs and benefits for the individual actors in any particular environment (above, also Maynard Smith 1974, and Maynard Smith and Price 1973). Societal complexity can generate situations in which wars could be escalated when such is clearly dysfunctional for some individuals, or even for the majority of the group. In complex societies, the interests of a soldier, a Pentagon general, and a State Department official are not identical; they may not even overlap. If humans have evolved, as Alexander and Humphrey argue, to assess the conditions around them, and to compete accordingly, there may arise situations in which, as part of an internal political competition, for example, troops are sent and resources committed to lethal conflict overseas. Thus the risk-taker, the front-line grunt, is paying a cost for the strategising of an unrelated but powerful individual, as a result of a conflict of interests that may have little to do with his own interests. As Hackworth (*Newsweek*, 24 February 1992: 24) noted: "Not many men in the mud are connected in high places."

Bueno de Mesquita (1981) developed an expected utility model of warfare, but his model does not calculate separately the costs and benefits of the various actors. He never examines the actual goals of the opponents in his disputes, nor whether the winners achieve those goals. In complex societies, an evolutionary ecologist would want to know what happens to the distribution of goods within the society as a result of war, and whether this is related to the occurrence of repeated war. Parker (1974, 1984) and Maynard Smith and Parker (1976) have examined these patterns. Consider territory- or harem-holding ungulates such as red deer. Clearly subordinate males will not challenge, but as the breeding season (rut) progresses and dominant males pay the price of vigilance with decreased nutritional status and health, challengers, who have spent less on maintenance of status, become ever more likely to challenge; the risks of real injury or death are greatest when the males are at roughly equal condition, but on opposite trajectories. In this ungulate case, the situation is relatively simple; the rut is seasonally limited, and a male's loss of condition as a result of his exertions over the rut period become evident as he begins to metabolize muscle tissue, something other individuals can detect from the odor of his urine.

## **Resources and Reproduction in Non-Human Species**

If we postulate that aggression is usually related to acquisition of resources, we must define "resource." The significant aspect of a "resource" in evolutionary perspective is its influence on survival and reproduction. Thus some biologists (e.g. Alexander 1979) define as a resource anything giving relief from Darwin's "Hostile Forces of Nature" — climate, weather, food shortages, predators, parasites, and so on. In this broad view, not only physical resources such as

food and shelter, but also status, coalition allies, and members of the opposite sex — potential mates — become resources. Though introducing complexity, this broad definition makes analytic sense, because the critical dependent variable is always differential survival (in order to reproduce) or reproduction. Because environments are complex, the focal resource will differ for different kinds of individuals (old, young, male, female, solitary or group-living). The job of specifying what resource is under consideration becomes critical.

Resources have repeatedly been shown to influence reproduction, even when only skill in resource acquisition, independent of social factors, is considered. For example, Ritchie (1990) demonstrated that optimally-foraging ground squirrels have approximately six times as many offspring as non-optimal foragers. For males of many species, there is a clear link between resource control or dominance status and reproductive success. The distribution (specifically economic defensibility), predictability, and richness of resources dictate the breeding system (e.g. Emlen and Oring 1977, Clutton-Brock and Harvey 1976). When resources are controllable by a single male, territorial systems are likely, and territorial males out-reproduce "bachelor" disenfranchised males. In non-resource controlling systems, while no physical resource of value may be controlled, more dominant males tend to out-reproduce less dominant males (reviewed by Dewsbury 1982, Huntingford and Turner 1987, Colishaw and Dunbar 1991). Males may fight directly over mates, they may fight for dominance if females choose dominant males, or they may fight over territory if females choose good territories.<sup>2</sup>

### **Resources and Reproduction in Pre-Industrial Societies**

What is the role of resources in human reproduction? As in other mammals, a sexual dimorphism exists. Males appear to be able to use large amounts of resources as mating effort to gain sometimes extraordinary numbers of wives and children (e.g. Low 1992; also Betzig 1986, who reviews despotic societies in which rulers may have thousands of wives and concubines). Females use smaller amounts of resources as parental effort, to raise a more limited number of healthy thriving offspring.

Cross-culturally, men use resources to gain reproductively; in many societies men's increase in reproductive success is accomplished through polygyny — additional wives. The majority (85%; Murdock 1967) of societies for which there are data are polygynous. When resource differentials are great, men, like other mammalian males, can use resources to increase their lifetime fertility to a much greater extent than can women. As in other species, status, skill, dominance, and power can be "resources," in addition to the things we commonly think of. Betzig's (1986) work shows definitively that in a number of societies, there are clear, formal reproductive rewards associated with status: high-ranking men have the right to more wives, and have significantly more

children than others. White's (1988) data on the Standard Cross-Cultural Sample reflect the fact that in a number of societies there are explicit rules granting more wives to political leaders, skilled hunters, shamen, and so forth. Even in societies like the Ache, in which there are no such formal rules, Hill and Kaplan (1988) found that skilled hunters have more wives, more children, and better-surviving children than other men.

In 10 of 12 societies reviewed by Hill (1984), resource control clearly enhanced reproductive success. The two exceptions were large, densely settled societies with socially-imposed monogamy. In most societies the relationship was quite straightforward: in the Turkmen, for example, Irons (1979 a,b) found that richer men had more wives and more children than poorer men. Borgerhoff Mulder (1988, 1990) found that in the African Kipsigis, richer men married younger wives and produced more children than poorer men (although with the introduction of western technology and medicine, differentials were reduced), and that women preferred to marry men with more land and no other wives. Among the pastoral Mukogodo of Kenya, Cronk (1991) found that wealth enhances reproductive success for men; in his study he was able to show the direction of causality. Similarly, the Meru use livestock for bridewealth, and richer men can marry more wives (Fadiman 1982); cattle represent wealth, and wealth represents access to women and thus ultimately, reproductive success. In societies as diverse as the Hausa (Barkow 1977), Trinidadians (Hinn 1986), Micronesian islanders (Turke and Betzig 1985), and Mormons (Faux and Miller 1984, Mealey 1985), status and wealth correlate with male reproductive success. Even in societies such as the Yanomamo, in which few physical resources are owned, male kin available for coalitions represent a resource, and men manipulate kinship terms in ways that make more women available for mates, and powerful men as partners (Chagnon 1982), so that reproductive success is uneven for men. Warrior status is directly related to reproductive success in the Yanomamo (see below).

Even in monogamous societies, monogamy may be far from absolute. In the Kalahari Bushmen, living in a resource-limited environment, 5% of the men manage to have two wives (Lee 1979). In nineteenth-century Sweden, certainly among the most egalitarian of states legally, resource-controlling men tend to out-reproduce poorer men (Low 1989b, 1990b, 1991, Low and Clarke 1991, in press). Voland (1990) found similar patterns in German villages, as did Hughes (1986) in England.

Thus even in relatively modern times, in Western societies which are monogamous and attempt to be egalitarian, wealth differentials appear to promote fertility differentials (Low and Clarke 1991, in press, Voland 1990; Turke 1989, 1990; Low 1989a,b, 1990a,b, 1991). When resources become constricted, (e.g. Low 1989a), family reproductive differentials are likely to disappear. Others also have found this generally to be true. Individual patterns in such important items as age of marriage typically vary with resources (e.g., Wall 1984; Sharpe 1990; Cain 1985;

McInnis 1977; Pfister 1989a,b; Thompson and Britton 1980; Hayami 1980; Schultz 1982; Symons 1974). Families may respond quite differently to such influences as market shifts, depending on their own resource bases (e.g., Galloway 1986; Schultz 1985), treat their children quite differently (e.g., Mitterauer and Sieder 1982:110). Even aggregate data tend to reflect resource influences, as individuals make decisions (e.g. Wrigley 1983a,b). Vining (1986) has argued that no such trends (richer men reproducing more than poorer men) exist in western society, do not consider lifetime fertility; they are thus difficult to interpret. Vining and others (e.g. Wrong 1980, 1985) argue that we do not know why, during periods of population expansion, wealth and status differentials correlate with reproductive success, and why these correlations seem to disappear when population growth stops. However, western technological monogamous societies today, including Sweden and the US, remarriage and second family formation may be sex-biased (men remarry more than women, and have children in second marriages more than women). When this occurs, men's reproduction is more variable than women's, and the society is effectively polygynous (Essock-Vitale 1984, Daly and Wilson 1983, Hartung 1982).

Low and Clarke (in press) suggest several possibilities why studies such as Vining's may fail to find patterns which may nevertheless be true. [1] First, census data are not designed to elucidate information about family lineages, but households (it is impossible to tell 'own' children, from stepchildren, from other relatives living in the household, from non-relatives living in the household); especially combined with inappropriate choice of measures, such data are highly unlikely to elucidate this relationship. In Vining's analyses, for example, (e.g. his Tables 2-5) proxy measures like education are used, rather than resources, and lifetime fertility is not measured; thus they are difficult to interpret. When actual lineage data are examined (e.g. Mueller 1991), wealth and status are likely to be correlated with fertility for men even today. [2] In many studies from earlier times, wealth was men's wealth. Today, much household income is earned by women. In industrial market economies, the effort which must be expended by women to earn money in market economies often represents a real conflict - a woman cannot do child care at work. This represents a real shift from women's situation in traditional societies, in which women could do a variety of tasks while doing child care; and in which women could call on older daughters to help during much of the day (not after school) with child care (see Rank 1989, Low and Clarke in press). [3] The ecology of infant survival, and of parental care effectiveness, also matter: when offspring must compete for limited resources, parental shifts from production of offspring to investment in offspring (MacArthur and Wilson 1967) will be favored. True parental investment, specific to particular offspring, must reduce the number of offspring, unless parental resources increase. [4] Finally, the existence of contraception is bound to complicate any relationship between wealth and fertility (Perusse 1991). Thus the link between men's resources and reproductive success may hold even today.

## **Conflict in Non-Human Species**

In most non-human species conflict is liable to be among individuals in the same population: red deer stags, elephant seal bulls, mountain sheep males, and so on, fight over reproductively important resources. In primates, male-male coalitions may be elaborated, and approach the complexity of politics (de Waal, 1982, Low 1990a, 1992). Thus conflict between groups of individuals from different local populations becomes important. In primates, defensive response to a behavioral challenge occurs in a number of species, in the contexts of territorial incursion, conflicts over a specific resource, including females (Manson and Wrangham 1991). It occurs in numerous group-living species. In chimpanzees, humans, and perhaps gorillas, there are regular cooperative raids by breeding adults against adults in neighboring groups. Manson and Wrangham argue that this is facilitated by social systems in which females change groups, leaving groups of related males behind. The complexity of such group raids may mean that its effectiveness is enhanced by intelligence (cf Humphrey 1976, 1983, who argued that the evolution of intelligence has been largely shaped by the social, rather than the physical, world; also Byrne and Whiten 1988, for a review of such Machiavellian intelligence). For this analysis, the important questions are: Does group-versus-group lethal aggression occur in species other than humans? Are the contexts (reproductive competition, kin selection) different from those of inter-group aggression in humans?

Among social carnivores, three species show inter-group aggression. In wolves, family-based packs occasionally invade neighboring packs' territories, attacking residents; Mech (1977) found that intraspecific conflict accounted for 43% of deaths not caused by humans. Among spotted hyenas, who, like wolves, live in family-based, territory-holding groups, intruders into a clan's territory are likely to be attacked and killed, and smaller clan sub-groups patrol the territory boundaries, confronting other "patrols" (Kruuk 1972). In lions, which also live in groups (prides) based on a group of related females and one or more associated males, inter-pride encounters occur, but lethal injury is rare. When invading males are attempting to take over a pride, there may be lethal injuries, though once one male cedes reproductive rights, aggression typically stops. New males are likely to commit infanticide (Packer 1986).

Adult male chimpanzees make aggressive forays into the ranges of neighboring groups, sometimes fatally injuring conspecifics attacked during these invasions (Goodall 1986, Goodall et al. 1979, Nishida et al. 1985). Unlike lions, chimpanzees may not stop attacks once victory is apparent. Females are semi-solitary, using a core area, but often travelling outside that area. Adult and sub-adult males are more gregarious and travel more widely (Goodall 1986, Nishida 1979). Total community size ranges from 20-110 individuals, but temporary groups range from 1-20 animals; group size fluctuates, and it is not predictable how many conspecifics one might encounter.

Further, in chimpanzees, it is more common for females to transfer from their natal group, while males are likely to remain among their relatives (Pusey and Packer 1987), thus changing the costs and benefits of risky fights. These factors have been suggested by Goodall (1986) and Manson and Wrangham (1991) as predisposing to "exported" aggression. "Reactive" aggression occurs in a number of primate species, including baboons, new world monkeys, lesser apes, and group-living prosimians (Cheney 1987).

Mountain gorillas live in small groups, with a single dominant male, and possibly one or more subordinate males. Both sexes may migrate from their natal group. Groups encounter each other often, and males with few or no females often "stalk" larger groups for several days. Harcourt (1978) reported that 50% of intergroup interactions in his study involved fights with physical contact; Manson and Wrangham (1991) relayed a personal communication from D. Watts of 15% in another study in the same area as Harcourt's study. Severe injuries and death may result from such fights. Gorillas do not, apparently, attack cooperatively (though the challenged male may get assistance from his subordinate males), and fights are not escalated if the victim yields.

Male-male co-operation, and the benefits of risk-taking, appears to be enhanced by groups of related males living together (called "male-bonded" or "female transfer" in primates, and "patrilocal" in humans); there is a statistical association between patrilocal residence and warfare in humans as well as other primates, for related men more often make war (Ember 1978). This is, however, not a requirement. In lions, males leave the natal group, while female relatives remain — yet lions engage in male inter-group lethal conflict. In gorillas, both sexes may leave the natal group. In wild dogs, wolves, and mongooses, both sexes are involved in lethal inter-group aggression. Each of these last three species has a monogamous, extended-family structure in which male and female costs and benefits are more similar than in polygynous species. The basic reasons for male-male intergroup aggression, rather than inter-group aggression by both sexes, probably involve the different reproductive payoff curves for the two sexes in mammals (above); the elaboration of this aggression is enhanced by conditions that result in related males living together.

In non-human vertebrates, then, most aggression, both inter-individual and inter-group, has a reproductive cause. Male-male coalitions are frequently among relatives, but may be among non-relatives. Males frequently come into open conflict over access to females, and control of resources useful in attracting females. Females may work in related coalitions to attack reproductive competitors, or the offspring of reproductive competitors (Wasser 1983, Silk and Boyd 1983). These situations typically involve harassment of subordinate females and infanticide, with little risk to the aggressors. Among primates, groups of males may fight in ways that resemble ambush attacks reported in preindustrial human societies.

### Peace-Making in Non-Human Species



In most of the species reviewed here, gestures of submission decrease aggression by the attacker. In chimpanzees, attacks may continue in the face of submissive gestures (de Waal 1982, 1989). Males form coalitions, fight single-handedly and in groups, and reconcile using vocal and behavioral signals of submission and alliance-seeking (e.g. de Waal 1982, 1989). Males have a formal dominance hierarchy, with far more aggression and reconciliation than females. De Waal (1989:53) suggests that the clear-cut dominance hierarchy provides a ritual format for reconciliation; reconciliations often follow a behavioral confirmation of formal status. Further (de Waal 1989:53): "the unreliable, Machiavellian nature of the male power games implies that every friend is a potential foe, and vice versa. Males have good reason to restore disturbed relations; no male ever knows when he may need his strongest rival." Later (1989: 61-69), de Waal gives a striking and poignant example of how male-male power tensions, unresolved, can erupt with lethal consequences.

An important distinction between all non-human species and humans is the lack of elaborate mechanisms in other species for ending inter- (as opposed to intra-) group conflict. While the patterns of reassurance, even negotiation, are sometimes present, these occur in resolution of disputes within the group. Thus, participants all already know each other, and have a high likelihood of continuing to live together. This argues that intra-group conflicts have been more frequent and selectively more important in these species' evolutionary history than inter-group conflicts. New complexities are introduced by the need to resolve inter-group conflicts in humans - among groups on individuals who may have information (or mis-information) about each other, but who may not know each other or be able to predict reliability or probability of default.

### **Conflict in Pre-Industrial Societies**

What are wars fought over in pre-industrial societies? Durham (1976), Harris (1979), and Divale and Harris (1976), suggested that wars were fought to secure scarce animal protein from the hunting grounds accruing to the winning side. However, Chagnon and Hames (1979) and Chagnon (1979) argued that it was not the means of production, but the means of reproduction, that led to such serious escalation of competition. In fact, what we call warfare in preindustrial societies is indistinguishable in context and function from much inter-group aggression seen in other species; it differs only in scope. Manson and Wrangham (1991) assessed warfare patterns in 87 societies, representing almost half of the standard cross-cultural sample, using warfare codes from Ross (1983). Approximately 60% of the sample societies engaged in warfare frequently - at least yearly. In a similar, and partially overlapping, sample Ember (1978) found that 64% of foraging societies fought wars at least once every two years. Warfare frequency was not related to subsistence type.

Most attacks in foraging societies were ambush attacks, not always with numerical superiority, and often well-coordinated to take advantage of the element of surprise.

Human societies are similar to other primates: individuals travel and work in small parties of varying sizes (Manson and Wrangham 1991). Thus escalation by larger groups can be fairly low-cost. Further, patrilocal and patrilineal societies are more common than other types of societies, and these conditions, involving as they do the association of groups of related males, influence men's costs and benefits of warfare. Similar patterns emerge in otherwise divergent societies around the world.

Chagnon's (1988) detailed study of Yanomamö warfare suggests that there can be direct reproductive advantages to men who participate in revenge raids and ambushes, and reproductive costs to men who avoid warfare. Yanomamö men who have killed on a war party are accorded the title of *unokai*, and a man's performance in war parties affects him reproductively. War parties are small, from 2-20 men, and tend to comprise related men. Although there are mystical aspects, most war parties arise from disputes about reproductive matters. Men may choose to avoid any particular warring party, and war parties may turn back, often as the result of a prophetic dream. Nevertheless, if a man avoids several possible opportunities, or behaves in ways perceived as cowardly on the raids, he becomes the butt of jokes, and other men may begin to make sexual overtures to his wife. Once a man establishes himself as *unokai*, he is likely to average one more wife than *non-unokai*, and will average 4.5 children, compared to 1.6 for *non-unokai*. There are clear reproductive advantages in the Yanomamö for men who participate in war parties, and particularly for men who kill (Chagnon 1988). Likewise, among the Jivaro (e.g. Karsten 1923), though there is no stratification, and during times of peace no chieftanship, when wars erupt, older experienced men who have killed many men and captured many heads are chosen as war chiefs. No Jivaro can be chosen if he has not killed. Bloody feuds are frequently "for the sake of the women," and follow familial lines.

In North America, the Blackfoot Indians were known through the nineteenth century as formidable, aggressive warriors (e.g., Denig 1961). Blackfoot warfare was "aimed at neither the systematic extermination of enemy tribes nor the acquisition of their territory" (Ewers 1958, ch. 7). Rather, numerous small raiding parties of volunteers banded together to capture horses from neighboring tribes; most parties composed fewer than a dozen men (though Ewers cited a few raids comprising up to 50 men), for reasons of stealth. Horses were used as brideprice. Ewers (1958) found that many of the most active raiders were men from poor families "ambitious to better their lot." Even sons of middle class families "needed more horses than their fathers could give them if they were to marry and set up their own household" (Ewers 1958). Occasionally a childless woman would accompany her husband on a raid. Horse-raiding parties were led by experienced men who were judged to have a good war record and good judgement. All participants were

volunteers, and though the leader might be a mature man in his thirties, most of his followers were in their late teens or early twenties. The youngest were considered apprentices, and given jobs such as holding the first lot of horses outside an enemy camp as the raiders returned for more. Unless prior arrangements had been made (e.g. equal distribution), each man could claim the horses he had led out of camp, or the range stock he had captured. Bitter arguments could occur over ownership, and it was the leader's job to settle these. Some leaders gave horses they themselves had captured to men who could claim no horses. A leader's generosity helped him maintain a popular reputation, helping him to recruit future followers easily. Successful raiders gave horses to their relatives, most commonly to their fathers-in-law or brothers-in-law (Ewers 1958).

Among the Meru of Kenya, geography fostered internecine conflict (Fadiman 1982). Livestock were used for brideprice; a man, to marry, must accumulate sufficient livestock (preferably cattle) to purchase a wife. Men fought to gain livestock and status. The military cycle followed the seasonal pastoral cycle. Negotiation of bridewealth was done by the families (principally male relatives; cf. Flinn and Low 1986) of the bride and groom, and inter-familial alliance was considered an important function. The father of the warrior transferred five specified items — a cow, a bull, a ram, a ewe, and a gourd of honey — to the father of the bride. Additional units of these and other items were negotiable, to sweeten the deal, but could not replace the basic five (Fadiman 1982:43,162). Additional symbolic gestures of alliance were involved (e.g. the warrior's father sending beer ahead of the actual brideprice, followed by the bride's father initiating a general beer-drinking to which the warrior's father was invited); however, a main point of the transaction was clearly economic. In fact, a portion of the bridewealth was often kept back by the warrior's family, often for years (Fadiman 1982:44). War was the principal method of gaining livestock, and warriors were expected to earn bridewealth as well as ever-increasing familial wealth and status. Rules and traditions of warfare among the Meru, in fact, facilitated rather than limiting cattle stealing. In individual conflict between warriors, for example, a warrior could save his life by declaring that his opponent could take his cattle; this was accepted as a declaration of surrender (Fadiman 1982:46). All captives, female and warrior, were redeemable for livestock. Married female captives could be kept as concubines or wives; unmarried and uncircumcised females were taken as "daughters," and later traded for brideprice (Fadiman 1982:44). Among the Meru, as among the Yanomamö, men clearly gained reproductively by establishing themselves as successful warriors.

The broad cross-cultural data are consistent with data from the Yanomamö, the Jivaro, the Blackfoot, and the Meru. Of the 75 societies analyzed by Manson and Wrangham (1991), reproductive matters were at the root of most wars. Women (abductions, failure to deliver a bride) were causes of warfare in 34 (45%) societies. Material resources specified as useful in obtaining a bride were causal in another 29 (39%), and in 9 of these, ethnographies specified that richer men

obtained more wives than poorer men. In only 12/75 societies (16%) was there no immediately obvious connection between warfare and men's direct reproductive striving. Divale (1973) although not quantifying the data or emphasizing the functional point of reproductive competition, also found that "among most groups it was adultery and wife-stealing" that caused wars. Similarly, in the full Standard Sample, women are captured in 66/158 societies (White 1988), and in the vast majority of these cases, women are married or kept as concubines by their captors. In other societies, like the Maori, in which there is no direct association between warfare and women or resources directly used to acquire women, the warfare patterns still reflect conflict over resources directly useful for the family line (e.g., Vayda 1960).

The benefits of warfare to men in preindustrial societies thus include increased direct access to reproductive females, and increased material resources useful for the lineage and in contracting marriages (individual [including sexual] and kin selection), and the communal location of related males (kin selection) appears to enhance warring behavior.

### **Transition in the Evolutionary Ecology of War: Societal Complexity**

Among pre-industrial societies, ambush warfare by raiding parties of varying size (almost indistinguishable from ambushes in other primates), appears to have been the common pattern. The rewards, as in other species, were reproductive: women as mates, and resources to purchase women as mates. The transition from such warfare to the complex multi-national warfare discussed in treatises on military history seems almost unfathomable, but must be examined if we are to understand whether there has been any change in the function of war.

The costs and benefits of warfare can vary. Among the Yanomamö, for example, a man's reproductive prospects are influenced by several things: his personal qualities, his ability to manipulate kinship terms (allying himself with powerful groups, making otherwise unavailable women nominally available as mates), the size of his kin group (male allies), and his prowess as an *unokai*, or revenge killer (above). Yanomamö society is not stratified, and aside from the size of kin group, men's chances for success may be largely under their own control. Individual men are rewarded in similar ways for similar war performances, and ferocity and leadership lead to reproductive gain.

Keegan's (1987) description of Alexander the Great suggests that even in large hierarchical armies during Philip's and Alexander's rule in Macedonia, personal characteristics, kin-group size, and ability to inspire loyal reciprocity still were crucial to success in warfare. The Macedonian kingship was elective; Alexander had claim to the succession, as the eldest son of the king's acknowledged wife, but, had he not been bold and eager for battle, he would have found it hard to press his claim. The period post-dated the "cavalry revolution" between the twelfth and fourth

centuries. Macedonia was an imperial power, and the Macedonian army was large and hierarchical, comprising a cavalry, the Foot Companions, light cavalry, light infantry, and specialized troops, including archers, siege artillerymen, engineers, surveyors, and supply/transport specialists. The soldiers were neither a tribal war band, as in the Yanomamö, nor were they conscripts. They were recruited from a variety of social classes. Nonetheless, central to the army was the inner core of warriors, the Companions, whose relationship to the leader was close, and often a blood relationship (Keegan 1987:34). It was important that Alexander consistently led his men, fighting by their sides, and performing dramatic feats of courage and leadership. Thus, while courage mattered among tribes like the Yanomamö, simply to avoid losing a wife, for example, in other cultures and by Macedonian times, heroism became a pre-requisite for leadership of vast and complex organizations.

Similarly, the transition to the state of modern Nepal, accomplished by Prithvinarayan Shah, owed much to his ability to reward individual interests. What is now Nepal comprised several small kingdoms; geographical constraints divided the area into small, self-contained units. Peasants' lives were hard. All land belonged to the state; those who worked the land typically paid half of the harvest to the state as well (Stiller 1973), as well as compulsory unpaid labor (*jhara*), even though few of the valleys were very fertile, with thin soils and poor harvests. Gaining a freehold was the only escape from this situation; it could be accomplished in three ways: a *jagir* grant (valid during the term of service), for services to the state; a *birta* grant (for a particular service, valid until revoked); or reclamation of waste land (Stiller 1973: 17-18). With only perhaps 8000-10000 men (Stiller 1973: 88), in the face of serious logistic problems, Prithvinarayan Shah drew men of the hill tribes, notoriously pragmatic and unlikely to follow others' dreams, into his ambitions, offering *jagir* grants for services as a way for followers to break out of the cycle of agricultural poverty that bound so many. Stiller (1973:94) argued that Prithvinarayan Shah spelled out in concrete terms the advantages for his soldiers individually, and drew them on to seeing the advantages of a farther-reaching group goal - true leadership. In addition, throughout the long campaign, in negotiating with his enemies, he offered substantial rewards for converting to his views — and was often successful. No other individual had been able to overcome the fragmentary relationships, and forge a modern nation from the region's tribes.

Leaders in war, then, had more likelihood of becoming leaders in peace. War has been proposed as a mechanism involved in the very formation of states. For example, Carniero (1970) argued that warfare was a necessary, if not sufficient, condition for the formation of states. Strate (1982) found a clear association between degree of central political organization and success in warfare. Otterbein (1970) found correlations between the level of political complexity and the degree of military sophistication (and likely success).

Warfare requires individual strife, and as noted above, strife is likely to be centered about matters of reproductive importance. Warfare further, at all levels above the simplest ambushes, involves organization and opportunities for gain through leadership; successful war leaders are likely to be good manipulators of others, and they accumulate an armed following. The path from leadership in war to political leadership may be short. The risks of political leadership, too, are sometimes less lethal than those of war leadership. Thus, the distinction between "pre-heroic" and heroic leadership (e.g. Keegan 1987) may be a matter of scale, rather than function. Recognition of the importance of reproductive interests in the evolution of lethal conflict, as I propose here, makes trivial some apparent discrepancies among earlier models of warfare and the rise of states. Thus, if competition can be driven to lethal levels by reproductive conflicts, it is no longer important whether population growth (e.g. Carniero 1970 vs Wright 1977, Webster 1975) is demonstrated to precede warfare. Reproductive competition is a major evolutionarily important selective force underlying lethal conflict; warfare is a principal mechanism, and may be waged in the name of women, revenge, agricultural lands, new territory, or any devised reason.

In hierarchical armies, the interests of the actors may diverge considerably, depending on their roles in warfare in more complex societies: the state leaders, the military leaders, support personnel, and the grunt on the front line. As societies become more complex, so does the scope of the problem. Axelrod and Dion (1988) have shown formally that increasing the number of actors makes cooperation more difficult; and "noise" (misperceptions, incorrect information) can invite exploitation. In fact, no strategy is evolutionarily stable if the "shadow of the future" is long enough.

It is not selectively irrelevant that, in all warfare involving hierarchies of power (i.e. rank and specialization; probably all but tribal ambush warfare), risk is correlated with prior status and/or rank. From at least the middle ages, it has been disenfranchised or low-status males who go to war in positions of greatest risk. Boone (1988) noted that sons of Portuguese nobles took three-week crusades to nearby, relatively safe locations, while sons of poor families went to Jerusalem, often dying there. Similarly, Dickemann (1979) found that it was disenfranchised males who went to war. And Moore (1991) found that among the Cheyenne, men who controlled more resources and had greater familial networks became peace chiefs; such men tended not to assume the risks of war. Instead, men who had no relatives, often simply orphans, became war chiefs; they could achieve some status, but remained unmarried. These war chiefs could gain the proximate rewards of status, but could not turn status into reproductive gain. The Cheyenne case appears to be an example of intra-group conflict of interest, between peace chiefs and war chiefs, with kinship and power on the side of peace chiefs. It would be extremely interesting to learn the history of the Cheyenne condition: were the first peace chiefs (political leaders) originally successful war chiefs who then discovered how to avoid the risks of leading war parties without losing status? Only when an

individual's other options are severely constrained, or he becomes convinced of some overwhelming benefit, should such extreme behavior be seen. Thus, the suicide missions of some Japanese in the second World War and the extreme risks taken in jihads in the Middle East should correlate either with otherwise very low status of the men, or with promises of gain unmatched otherwise.

Shaw and Wong (1989) argued persuasively that kin selection still drives much conflict even today; this is why, for example, when societies are very large and comprised of diverse groups, intra-group or ethnic conflict once again becomes important — civil war is more common than international war (also, see below). If lethal conflict has an evolutionary context of reproductive striving, then inter-national wars seem unlikely to be anything other than epiphenomena, although leaders may use tactics of referring to proximate cues important in evolutionary time (familial terms to promote patriotism, etc). Real strife over local resources seems most likely to escalate into lethal conflict -- and indeed, civil war and ethnic strife are far more common in nation-states than international war.

### **Greek Hoplites: Early "Western" Warriors?**

Hanson (1989) argues that classical Greek warfare has "left us with what is now a burdensome legacy in the West: a presumption that battle under any guise other than a no-nonsense, head-to-head confrontation between sober enemies is or should be unpalatable" and that the Greeks provided the first real shift in the West, at least, away from small band, guerrilla ambush attacks (the usual pattern in pre-industrial societies). Indeed, the Greek situation shares some characteristics with modern war, but it also shows some important, and perhaps underappreciated, differences.

The rise of the hoplite — a heavily armed and armored infantryman — in warfare during the second half of the seventh, and the sixth, centuries B.C., had important political as well as military consequences (McNeill 1963). Hoplites fought in phalanxes, and each man's life depended "upon the stalwart behavior of his neighbor in the battle line" (McNeill 1963:198). For the most part, hoplites were small farmers, and the agricultural constraints of vineyards, olive groves, and grainfields meant that battles were fought during the summers by local farmers to gain or protect local property (Hanson 1989). In most city-states (except Sparta), there was little combat specialization and very limited drill (Hanson 1989: 120). Men were vulnerable to the draft in any summer from their 18th to their 60th year, and in any battle, the majority of men were likely to be over 30 (Hanson 1989: 90). Men of rank fought as ordinary hoplites among their less noble neighbors, and men fought with others of their tribal affiliation. When columns were decimated, they were not immediately reconstituted, but men simply moved over to take the place of a man killed — usually a friend, relative, or neighbor (Hanson 1989: 122) Thus the survivors of a battle

were likely to know all of those killed. Men testified to the numbers of battles others fought, a sort of mutual recommendation system that Hanson (1989: 123) characterized as a "rather intensive mutual interest." Men fought, then, with their kindred and their neighbors, with whom they held many interdependent relationships. Strong bonds were reinforced. Even the famous homosexual bonds of Spartans and the Sacred Band of Thebes had military impact (e.g., Hanson 1989: 124).

Thus, while these conflicts (like others of the times) involved trained warriors in organized combat, rather than tribal ambushes, individual men were still fighting to protect (or gain) their own land resources, and they fought with their families, tribes, and neighbors. Shared interests were immediate, local, and often kin-based. Commanders fought in the front lines with their men, suffering almost certain death if defeated, and perhaps surprisingly, a relatively high proportion of victorious generals died. Hanson (1989) suggests that these patterns result from the crucial importance to troop morale of a general fighting at the front, being among the first to face the spears of the enemy. In contrast, in most modern wars (e.g., Keegan 1987), commanders have moved further from the front lines, and share fewer risks with their troops (with some notable exceptions in the American Civil War).

### **The Evolutionary Ecology of Renaissance War**

War in the Middle Ages, up until mid-fifteenth century, involved many small-scale territorial wars, and local powerful men — a sort of "violent housekeeping" (Hale 1985:13). Knights, up until perhaps 1450, fought largely as individuals (Hackett 1983:28). Typical causes included revival of old family claims to previously lost estates: "political Europe was like an estate map, and war was a socially acceptable form of property acquisition" (1985:22). While particular causes differed, familial economic interests were clearly present. Noblemen, landed gentry, had strong vested interests in waging warfare, not only for reasons of territory defence or acquisition, but for the spoils and riches gained from plunder and ransom. Interestingly, it was later-born sons who tended to end up in high-risk warfare (Boone 1988)

Kinship-mimicry was also used: military adventurers often became *fratres jurati*, sworn brothers. When William the Conqueror invaded England, Robert de Oily and Roger de Ivery were *fratres jurati*. Receiving honors for battle, Robert gave Roger one as his sworn brother. Fifteenth-century *compagnies d'ordonnance* (Hale 1985:92) engaged the monarch's personal interest, and were a route to high administrative office, confirmed disputed titles, and paved the way for handsome plunder of ransom profits.

The introduction of guns permanently changed the nature of war, its conduct and conditions. At some level, of course, it is fair to say this of any technological development, any new war tool: horses (Newark 1979), crossbows (McNeill 1982). But gunpowder may have had



an unforeseen impact that fed back into the nature of selection on warfare. Gunpowder led to larger and more costly armies, with more support personnel (e.g., masons to make balls of stone if the iron ones ran out). It led to longer-lasting conflicts (previously limited by an individual's ability to exert sustained physical effort). It changed the nature of confrontation (guns could be poked through holes in fortifications). Sieges became more common. Perhaps most important, it changed the requirements for soldiers: it took far less skill or resources to fire a musket than to train as a longbowman or cavalryman. This separated the risk-bearers from those who could profit from warfare. Further, a new group emerged: weapons-makers, with complex skills and political power, who could profit from lethal conflict without the risk of engaging in it (see McNeill 1982).

Increased costs were passed on to the population in the form of higher taxes, and in "voracious" recruiting, although field armies probably never drew on more than 5% of the population (Hale 1985:75; taxes become an important issue in all but the most local wars; see also Miller 1975, and Elton 1975). Mercenaries became prominent. Efforts to intensify involvement of the landed gentry were not too successful, for predictable reasons: percentage quotas, rather than individuals (except in the case of personal indentures; Hale 1985:77) were drafted, and those who could buy or litigate their way out of the draft passed the burden on to those with fewer resources. Early in the period, substitutes were liable to be younger sons of nobility, but later substitutes were those without skills, poor, and hungry, even on the run from criminal proceedings. Hale (1985:109) quotes the Venetian commander Giulio Savorgnan in 1572, regarding why his troops had enlisted: "To escape from being craftsmen, working in a shop; to avoid a criminal sentence; to see new things; to pursue honour — but these are very few. The rest join in the hope of having enough to live on and a bit over for shoes or some other trifle that will make life supportable." Similarly, in 1600, Thomas Wilson assessed English forces (Hale 1985:125) as comprising chiefly cottagers and copyholders, but also those who are "poore, and lyve cheefly upon labor, workeing by the day for meat and drinke and some small wages."

Renaissance wars, then, were fought by mercenaries; the standing army came into being after the Renaissance (Chamberlain 1963:143). The power held by those possessing desired skills passed largely to others, not those who fought. Further, mercenaries had impact on civilians during peacetime: unlike knights, who were likely to return home, or paid soldiers, responsible to their employers, mercenaries during peacetime were "the responsibility of no man and they consequently became bandits" (Chamberlain 1963: 151).

Over time, then, the potential individual reproductive gain of warfare fostered technological innovation, and then the technology of war changed the nature of warfare itself. The balance of benefits seems to have shifted, for most actors, from a familial, resource- or status-building strategy, as in the Yanomamö, the Meru, and Europe of the early middle ages, to a more stratified situation in which the poor and disenfranchised began to shoulder the risks and costs of warfare —

as in the Cherokee, Portuguese nobles, and even Vietnam. A shift occurred, in which more expertise was required for the manufacture than the use of common weapons, further separating the risk and the costs for warriors. Of course, it's hardly so simple; rewards and booty remained important resource advantages for some men. Even today, it would be difficult to disprove an accusation that individual fortunes and family empires are sometime built from war, but the range of variation in advantages available for warriors appears to have increased, and non-warriors have entered the equation.

### **The Evolutionary Ecology of Modern War**

It is almost certainly true that past correlations between warriors' behavior and reproductive success no longer hold; certainly the necessary data, with appropriate controls, are lacking. Nonetheless several aspects of men's behavior in wars, and of the organization of fighting forces, suggest that [1] **proximate** correlates of reproductive success due to risky and aggressive behavior still exist in modern wars, and [2] successful leaders organize field units in ways that play on past kinship structure of warring groups.

#### Training

Many features of the training of young men for warfare mimic the proximate cues of both kin groups and close reciprocity. It is common for new recruits in many armies to undergo forced transformation to uniformity (GI haircuts, uniforms; e.g. Holmes 1985). Their training emphasizes communal values, often by using kinship terms; training is aimed not only at obvious skills; as the sheer size and complexity of warring groups increases, training aims at ensuring cohesion, inciting hostility, enforcing obedience, and suppressing mutiny (e.g. Holmes 1985, Dixon 1976). Recruits are likely to be called "son," "boy," or "lad." As Holmes (1985: 46) notes, this paternalistic language goes far beyond basic training, and has done so for centuries. The "sworn brothers" fighting together in the Middle Ages also represented reciprocity bolstered by mimicking kinship.

Hackworth (1989:633-5) argued that a significant portion of the combat failures in Vietnam arose directly from a limited number of causes, including poor training that broke the pattern Holmes reviews. Instruction was done by returned short-timers who had not wanted to go to Vietnam in the first place; dissatisfaction often led to war stories rather than training when supervision was absent. Perhaps most significant, men were not trained and put into combat in units, with their mimic of familial structure and their strongly developed reciprocity; rather, men were sent individually into combat; in a strange land (the finishing preparation for this jungle war

was done on snow-covered fields), without the required skills (e.g. none of Hackworth's trainees could answer what to do when the gun jammed), and dependent on strangers, many died.

### Pre-Battle Exhortation

Successful commanders from time immemorial have played upon the major themes of gain: not only economic, but reciprocity and the powerful pull of kinship and sexual selection. Thus Du Guesclin, a French knight of the mid-fourteenth century, mixed penitential motives with profit, when he urged his recruits (cited in Gies 1984:157): "If we search our hearts, we have done enough to damn our souls . . . For God's sake, let us march on the pagans! . . . I will make you all rich if you [follow me]!" Interestingly, Hugh of Caveley, an English knight fighting with him, responded by invoking kinship and reciprocity: "Bertrand, fair brother and comrade, mirror of chivalry, because of your loyalty and your valor, I am yours, I and all these here." Shakespeare captured the essence of this strategy, when he had Henry V, before Agincourt, first recite a litany of famous and powerful names, then exhort his rag-tag collection of men, calling them brothers even while highlighting their class diversity. The folks at home are sometimes similarly exhorted. In the recent news headlines of the Middle East conflict, headlines reinforced kinship images: "Shipmates become like brothers in Gulf pressure-cooker (Detroit News and Free Press February 10, 1991).

### Resistance to Interrogation

Watson (1978; also see Hackworth 1989) makes an important point about the importance of group structure and intra-group reciprocity; he notes, for example (1978:298; also Schein et al. 1957) that during the Korean war, the most successful North Korean interrogations followed breakdown of the prisoners' group structure. Thus reliable group structure - the presence of dependable comrades-in-arms - contributes not only to desired behavior in battle, but increased ability to resist interrogation after capture.

### The Role of the Disadvantaged

War has changed. From the engagement of relatively few (often related) men in individual combat over resources directly related to their lineage's success, armies have grown and become hierarchical, with increasing divergence of interests of the actors. From related men who might squabble over this bride or those cows, we now have administrative groups sending others to fight.

Maintaining discipline and loyalty in the face of unequal payoffs can be tricky. Alexander (1979) argued that this problem lies at the very root of the transformation of societies from often

highly polygynous states to (at least relatively and prescriptively) monogamous states. In polygynous societies engaged in large-army warfare and conquest, formal reproductive and resource distribution schemes are common.

As warfare technology changed and armies became larger, status differentials increased. No longer, as among the Yanomamö, were the spoils of war a relatively simple reflection of individual courage and skill. More high-status men opted out of conflict, and more low-status men were recruited or drafted. These men, from at least medieval times (Boone 1988) to the Vietnam war (Hackworth 1989: 634) suffered higher casualties than their richer competitors.

Hackworth (1989:634) called the failure to mimic the familial structure of pre-industrial warfare (which resulted in high casualties and an increasing need for replacements, followed by a lowering of induction requirements) "the most blatant example of the use and misuse of the poor and disadvantaged in America's wars/ These men, the Project 100,000 soldiers, were those who had (or would have) previously failed the armed services' physical or mental requirements; they proceeded through the Army "as they proceed through life, walking wounded in the center of a monstrous joke, forced to struggle with basic training as they are forced to struggle with everything else (Just 1970:62). The Vietnam example may simply be the most recent and extreme case; Watson (1978: 34) reviews a 1960 PRB Technical report showing that the more intelligent, able soldiers, the better fighters, cluster in the safer jobs, away from the front line; Watson calls this "Catch 23."

Yet the fate of disadvantaged men is not so simple; if it were, the only question would be why any ever serve. Just as the costs and benefits for any individual of living in a group must be weighed against the costs and benefits of living alone or in another kind of group (e.g. Alexander 1974), the question must be asked: Did these men, on average, fare better or worse than if they had remained civilians? No data exist. For those who survived, it is possible that they did in fact fare better than if they had not served, through the status of wearing a uniform (cf. Holmes 1985:93).

### Insurgency and Terrorism

In evolutionary terms, individuals and groups should engage in potentially lethal conflict only when the net reproductive outcomes are likely to be positive. Gunpowder is one example of a technological change with great impact on these costs and benefits for the primary actors — warriors. Technology has another effect: as the lethality of weapons increases, a small number of people can threaten stability or lives of large numbers of people (e.g. Wilkinson 1986). As major powers shy away from escalation of international conflicts most likely to lead to nuclear engagement, local, usually ethnic, conflicts become more important, and as the technology available

to small groups increases in sophistication (SAMs and heat-seeking missiles have been captured), the danger posed by small groups increases.

Reviews of contemporary terrorism (e.g. Gutteridge 1986) and low-intensity conflict (e.g. Klare and Kornbluh 1988) suggest that despite exceptions like the Red Brigade, most conflicts in fact originate as local ethnic or religious conflicts of interest —e.g., the Basque struggle, Northern Ireland, the West Bank. Conflicts like these probably are intensified by the sorts of pressures prevalent throughout the evolutionary history of warfare: genetic lineages in conflict, expanded to become regional conflicts (see Shaw and Wong 1989 for good discussion of several such conflicts). It is probably not irrelevant that in many successful (long-lasting) terrorist groups, the leader assumes a paternalistic role, and the group structure mimics that of families (e.g. Aston 1986). However, as Wilkinson (1986) points out, a major "growth" area in terrorist activity is the expansion, allowed by technological advances, of basically local ethnic and religious conflict to international scale. Some patterns are evident: kidnappings are more likely on "home" territories, barricades and hostage-taking elsewhere (Aston 1986). In western Europe, there is an ethnic bias to kidnappings (Aston 1986). Even a review of larger-scale conflicts suggests that ethnic and racial components are still important after World War II — far more important than ideology or nationalism (e.g., Brogan 1990, Keegan and Wheatcroft 1986, Dunnigan and Bay 1986). The current tensions in the Middle East speak clearly to this point.

The real danger is probably that small, originally local conflicts, because of technological advances, can wreak international havoc, and major powers can then be drawn into the fray. For example, Goose (1988) notes that U.S. funding for Special Operations Forces, typically involved in low-intensity interventions in local conflicts, increased 100% during the 1980s. There is real potential for major powers to be drawn into confrontation through (originally) local conflicts (Maechling 1988), and balancing such conflicts can impose high costs and real risks (Barnet 1988).

### Deception and Warfare

In other species, aggression is accompanied by advertisements that exaggerate an individual's prowess (e.g. Alexander 1987). In human conflicts, there are probably not qualitative differences, but it may be that there are important quantitative differences, compared to conflicts of other species. We may be capable of more subtle deception; this in turn may in fact make conflict more, not less, likely, because conflict is more likely when at least one contestant's information is faulty (Parker 1974, Alexander 1989:239, above). In human arms races, Alexander (1987:239) argues, secrecy, deception, and misinformation are necessary; otherwise there would be unpredictable occasions when the stronger party might simply use its force (that there exist examples of precisely this tactic merely shows that bluff doesn't always work). The outcome of

this requirement for secrecy and misdirection, argues Alexander, is that policy makers and government officials must often oppose citizen concerns. This situation is complicated by the fact that leaders and their advisors play a double game, both laterally, with other national leaders, and vertically, with the public, and the influence of the public on leaders' policies is maximized only periodically (in the U.S., every four years), and the public has imperfect, manipulated information.

### War and Reproduction

In pre-industrial societies like the Yanomamo and the Meru, a man's lifetime reproductive success was likely to be closely correlated with his performance in war. Nor are these two examples atypical; in many societies, reproductive rewards for valor were standard (e.g. the Comanche, Cabello y Robles 1961:178; the Natchez, Swanton 1911:104). Both direct reproductive rewards and status or privilege before the law were common rewards for leadership and success in war (e.g. Betzig 1986).

As armies became larger and more stratified, and as direct formal reproductive rewards for performance disappeared, the situation becomes far less clear. The origins of this shift appear in Renaissance warfare. For many, there are obvious risks, but no longer obvious reproductive rewards. For disenfranchised men, with little or no chance of success in peacetime environments, there is possibly a correlation (above, Holmes 1985), but it is hard to measure.

### **Proximate and Ultimate Causes of War: Evolutionary Novelty**

Warfare evolves to be common only in circumstances in which the net fitness of warriors has been enhanced. Reproductive costs and benefits, and conflicts of interest, are central. In an evolutionary sense, the ultimate causes of war, as of all lethal conflict, are sexual selection and kin selection. Throughout the animal kingdom, lethal risks are taken only when the reproductive stakes are high. Individuals and groups of related individuals, principally males, fight over mates and resources important to reproduction. Groups of chimpanzee males attack each other in ambushes very similar to those in pre-industrial societies. Sexual selection and kin selection are the driving forces creating the reproductive rewards that make the risk of death worthwhile; kinship and reciprocity are the principal binding forces among those who fight together.

With the elaboration of war, and the increased pace of weapons development, selective outcomes became less tied to individual actions and characteristics. Those with the most to gain from warfare frequently suffered lower risks than those with little to gain. We may well have unhooked the reproductive rewards from the behavior, so that lethal conflict is now counter-selective, and driven only by proximate cues, but throughout the evolution of conflict in humans as

well as other species, there have been reproductive profits associated with the risks of lethal conflict. Now, perhaps, though there are no data, war may not profit anyone directly involved in the conflict — but the driving cues remain.

With this in mind, let us review very briefly some of the proximate causes of warfare assigned in modern conflicts. This subject is far too broad for a detailed analysis here; the specific causes are multifarious; others (e.g. Singer 1980,1989, Huth 1988) deal with it in more detail. There are, however, some major patterns uncovered by others that may be well worth reviewing briefly here. Consider for a moment some of the causes and correlates of war: number of contiguous neighbors (Richardson 1960), economic conflicts (approximately 29% of wars 1820-1949, Richardson 1960), territory disputes (Richardson 1960), ideological differences (Winter 1989), and misperception or distortion of information (wars in this century, Stoessinger 1982). Pacifying influences include shared ethnicity (Shaw and Wong 1989, Richardson 1960), common government (Richardson 1960), recent alliance (Richardson 1960), and extended deterrence when military strength is sufficient in the short term (Huth 1988). Stoessinger (1982) and Winter (1989) note the important potential impact of leaders' personalities. Even in the huge number of specific causes of wars in modern times, the "ecological" categories are still rather limited: conflicts arise over resources (economic or territorial), and are less likely the longer and deeper are common bonds (kinship or reciprocity); open conflict is often precipitated by faulty information.

There is, however, a behavioral ecology of war in our evolutionary past. The multiplicity of proximate correlates in modern warfare does not mute the importance of the ethnic (and perhaps male competitive) forces. Brogan (1990) counts at least 80 wars since 1945, resulting in 15 to 30 million deaths. The vast majority of these, he finds, are between peoples and races; few are international or ideological. A review of other recent atlases of war (e.g., Dunnigan and Bay 1986, Keegan and Wheatcroft 1986) reinforces the importance of essentially tribal conflicts of interest.

### **Can Evolutionary Theory Help Avert Arms Races?**

If potentially lethal conflict has very old evolutionary and ecological roots, can learning about these roots help us avert arms races? It is difficult to tell, but perhaps a knowledge evolutionary theory can help us mitigate and control them. Understanding the evolutionary background of lethal conflict and arms races may simply help us to understand that costs and benefits, deception and misperception, may involve currencies other than the immediate and obvious ones (cf Stoessinger 1982).

Shaw and Wong (1989: 204-208), in their analysis, review both the hope held out by evolutionary theory, and the barriers to its usefulness. Sadly, after the eloquent analysis of their entire work, they are reduced (1989: 208) to calling for "some form of world government, some

management force that might stabilize the most immediate threat to humanity — nuclear destruction." Their entire work, however, is an acknowledgement that the power of in-group amity and out-group enmity would likely force any such world government to be a conquest state, a chilling prospect.

If the data reviewed here are correct, warfare evolved in circumstances in which mating and thus fitness benefits were worth lethal risks. We now have largely broken that link, but we, like other organisms, have not evolved to "calculate" ultimate (lineage) results, but to respond to proximate cues. Now, the reproductive profits may be largely gone, but the proximate cues remain. Writing of just such problems, Alexander (1987:240), found that "It seems to place me in a camp of those who see mutual deterrence as the basis for peace, even though I doubt that either self-extinction or massive destruction can be prevented indefinitely by deterrence alone." He then suggested that, given our finely honed social and predictive ("scenario-building") intellect, several partial brakes on arms races may exist. — e.g. if sufficiently numerous and powerful individuals and groups perceive that no matter who wins the confrontation, we all will lose, their power in internal social/political coalitions may allow them to force some solutions. The difficulty is that the brakes are weakened by the dilemma a biologist would call the "levels of selection" problem: because natural selection works in the genetically selfish ways described above, long-term costs and benefits to groups are discounted compared to immediate, short-term costs and benefits of the individual. The larger and less related the group, or the farther in the future costs and benefits must be calculated, the greater will be the discount. Thus, given a short-term gain in status or tax base for a local constituency versus an unspecifiable risk of nuclear warfare some time in the future, we do not predict restraint.

Any attempt to foster peaceful behavior must change individual costs and benefits in the proximate sense (e.g., Goldstein 1989); as Groebel and Hinde (1989) note, currently many social institutions and rewards mediate strong status pressure on individuals to enter into wars. This sounds simple enough, and has parallels in economic approaches, but the following difficulties are serious: (1) unlike small-scale societies, there are no longer easily-identified, powerful groups/coalitions with focused costs and benefits, so it is hard to figure out how to direct any such proposed manipulations; (2) now, to an extent previously unknown, small groups of individuals can control highly destructive devices. When these individuals are unaffected by the sorts of costs and rewards humans have evolved to recognize, we call them terrorists. Our technology is sufficiently advanced that even such small groups can wreak havoc, killing great numbers of people.

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#### Notes

<sup>1</sup>A caveat is important. Because a trait exists, even if it has a current positive impact on fitness, does **NOT** necessarily mean that it is an adaptation (Williams 1966). It is, in fact, an onerous task to demonstrate that any trait is an evolved adaptation: we must show that the trait not only correlates with some environmental condition, but is effectively **designed in response to** that condition. Behavioral and evolutionary ecology focus on the correlations among environmental circumstances, behavior, and inclusive fitness. We may see, particularly in complex systems, non-evolved effects of behavior that had originally an entirely different function. In such cases, we must distinguish between the questions "What is the evolutionary history of the trait? Is it an adaptation?" and "What, in terms of fitness, is the current utility of the trait?"

<sup>2</sup>Two of the best-documented examples of the behavioral ecology of reproduction, and the role of conflict and resources in reproduction, are Clutton-Brock et al.'s (1982) work on red deer, and Le Boeuf and Reiter's (1988) work on elephant seals. In elephant seals, males mature later than females, and grow to be much larger than females. Over 85% of all males ever born die without issue, but the most successful males may have over 90 offspring. Variance in reproductive success among males is extreme, whether measured seasonally or over lifetimes (Le Boeuf and Reiter 1988), and the reproductive stakes are much greater for male fighting than female. Approximately 60% of females ever born die without giving birth; the most successful females may have about ten offspring in their lifetimes. Males compete for the control of sandy beaches on which females give birth, and fights can be severe. Seal pups are often injured and killed as males fight. Because females return to the same or nearby beaches every year, but male tenure changes, the probability that an infant killed is the offspring of the territorial male is difficult to determine.

In red deer, adult males may be bachelors, with no females, or they may control a harem of from one to more than 20 females (Clutton-Brock et al 1982). Harem holders do virtually all of the breeding with the hinds in their harems. However, because the tenure of harem-holders is shorter than the breeding season, reproductive success of males does not vary so much as harem size. Variation in reproductive success among stags is a function of harem size, duration of harem-holding tenure, rutting area, fighting ability, and (less closely) life span. Stags achieve harem-holding status and matings through fights. Big, long-lived stags who are good fighters leave the most offspring.

Among females, variation in lifetime reproductive success is related to life span and calf mortality. Variation in fecundity is small, and less important than for stags. Thus, for stags, size and ability to gain dominance are crucial; for hinds, own and calf survivorship is important. The impact of different amounts of resources for the two sexes is quite different, and as is generally true, male red deer reproductive success varies more than female reproductive success. Both well- and poorly-invested hinds can be successful producing offspring; the reproductive impact of resources is far less for hinds than stags. There is a complication. Male calves that are born early in the season (with a long time to grow before their first winter) and at a high birth weight are more successful than those born "late and light." Not surprisingly, the sons of dominant hinds, in good condition, are more likely to be born heavy and early (Clutton-Brock et al., 1986). Sons of

dominant hinds have greater reproductive success than daughters of dominant hinds; daughters of lower-status hinds had greater reproductive success than sons of low-dominance hinds. Further, dominant hinds produced more sons than low-status hinds (Clutton-Brock et al 1986). Dominance in hinds is related to their own birth weight, and their weight as adults. Thus resources are not irrelevant for hinds' reproductive success, even though the impact is less than that on stags, and may be seen more strongly after a generation's lag, in the sons' success.

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