university of groningen

## University of Groningen

## The origin of war

Dennen, J.M.G. van der

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1995

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Dennen, J. M. G. V. D. (1995). The origin of war: the evolution of a male-coalitional reproductive strategy. s.n.

## Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

## 1 The Origin of War: Introduction

### 1.1 Why the Interest in (Primitive) War?

When I embarked upon the enterprise of collecting literature on human primitive war some 15 years ago - with the objective to understand the origin of this puzzling and frightening phenomenon of intrahuman, intergroup killing - little did I suspect that some ten years later that subject would be very much alive and kicking in disciplines as diverse as cultural anthropology, ethology, evolutionary biology and sociobiology, and the socio-ecological branch of primatology, generating an abundance of novel and intriguing theories, engendering new waves of empirical (cross-cultural) research, and lots and lots of controversies.
At that time, the question of the origin and evolution (if any) of human warfare was a totally marginal and neglected domain of investigation. Among polemologists (or peace researchers as they are known in the Anglosaxon language area), there seemed to be an unshakable consensus that war was a cultural invention and social institution, which had originated somewhere in Mesopotamia some five thousand years ago (It actually was, and still is, a curious blend of the credos of the Margaret Mead school of anthropology, the simplistic dogmas of behaviorist psychology, and a historicist sociology - all consenting to the tabula rasa model of human behavior, i.e., the assumption of infinite plasticity and sociocultural determinism - inexplicably mixed with assumptions of a static Human Nature derived from the Realist school of political science). Such a conception precluded any evolutionary questions: war had a history and development, but no evolution in the Darwinian sense.
My main field of interest at that time was all aspects of animal and human aggression and violence, especially the collective and organized violence known as war. For most polemologists, including myself, this meant, in fact, studying contemporary warfare, i.e., from roughly the Napoleonic wars to the Vietnam war. Others regarded only the post-World-War-II wars or the Cold War to be of any scientific relevance. I gradually became interested in the study of 'primitive' war (i.e., warfare in nonliterate, prestate-level societies) for several reasons:
(1) It was not unusual at that time (nor is it now) to point to the alleged ubiquity and universality of war as somehow conclusive evidence of human 'innate aggression', or some other evil streak in human nature. I have always felt extremely unhappy with such a notion, which has a strong foothold in western Christian tradition, and I decided, if not to refute, at least to challenge
it.
(2) I also gradually discovered that the wisdom of the age in regard to primitive war was sadly unsatisfactory, highly stereotyped ('noble' versus 'ignoble' savage), and totally inadequate for theoretical propositions beyond the cocktail-party-wisdom level. This was the main reason to start the Ethnological Inventory Project: a compilation of the warring/feuding behaviors (or absence thereof) and motives of all the societies ever described in the ethnological and ethnographical literature, as much as possible based on original sources ${ }^{1}$. Some preliminary results of this ongoing research have been reported in van der Dennen (1990, 1993), and Ch. 7.
(3) And last, but not least, I soon found myself absorbed in the subject matter, sucked into the maelstrom, intrigued, indeed, fascinated for its own sake. How was this all possible? How did war originate? And - perhaps above all - WHY?

While I was frenziedly skimming all the literature I could lay hands on in search of some solution, some hint even, to the vexing problem of why human beings - 'primitive' or 'civilized' did not seem to make a difference - exhibited this peculiar behavior of massively and concertedly exterminating members of their own kind, two things happened which changed my perspective dramatically. The first was Jane Goodall's reports in the seventies - in the first reports her despairing bewilderment about the discoveries is clearly perceptible - of strange and horrible events happening in the chimpanzee population she had been observing for many years. Some of her beloved animals seemed to have acquired a taste for cannibalism, and, incredibly, one community of chimpanzees actually seemed to be trying to deliberately exterminate another community, in such a way as to closely resemble human raiding in warfare. Obviously, Homo sapiens sapiens was no longer unique among the creatures that crawl this earth in its destructive propensities. Equally obviously, all theories about the origin of war, in which implicitly Man's uniqueness was presumed, could be put quietly to rest. A broader, more general explanatory perspective or framework was required: an evolutionary one.
The second change which had an impact on my thinking occurred gradually. What had at first looked like bedazzling, kaleidoscopic diversity - all these different cultures and diverse societies, almost limitless in their variability of behaviors, customs, values and world views - gradually turned into a much more coherent view of rather superficial variations on a common theme. The

[^0]common theme we might as well call human nature', the variations stemming from the contingencies and bric-à-brac of the material culture and the social cosmologies of the peoples involved. What gradually emerged was the constancy beneath the superficial differences, the communality beneath the variations; it dawned upon me that all these variations were indeed variations on a common theme, and that this common theme must be something like a universal psychology. There was only one theory which could accommodate this new insight: evolutionary theory.

In the remainder of this chapter, I shall us the term sociobiology as a shorthand for evolutionary biology, socio-ecology, ethology, Darwinian psychology, and similar disciplines, with the emphasis on evolutionary biology and Darwinian psychology.
Why a sociobiological approach? Some critics would object that it is unethical or immoral (it should not be done); others that it is irrelevant (it's a dead-end street). For many people, including myself, war is an abhorrent subject to deal with in the first place; and sociobiological explanations being in themselves detestable, sociobiological explanations of warfare are, so to speak, repulsive to the power two ${ }^{2}$.
My own position is that the questions sociobiology poses are relevant, legitimate and valid. But whether sociobiology can provide valid answers to these questions is another question altogether (Cf. Voorzanger, 1987). That is, among other things, what I intend to investigate in this study.
One caveat is in order: there is no such thing as the evolutionary-biological theory. Rather it is a collection of premises, (sometimes contradictory) hypotheses, and islands of theory formation: a paradigm in statu nascendi. What these have in common is the assumption that Homo sapiens sapiens (Man, for short), like all other organisms, evolved, and that at least part of his behavioral repertoire can be understood in an evolutionary perspective. There is no compelling reason why selection and evolution should be confined to operate only on the morphology and neurophysiology of organisms. Those readers who are convinced that human social behavior is somehow beyond evolutionary explanation, I sincerely recommend not to waste their time reading this book, as I shall make no attempt whatsoever to convince or convert them ${ }^{3}$.

[^1]Let me qualify my own position as 'methodical skepsis', which means not only skepsis about methods, but skepsis as a method, as the only way to avoid traps, pitfalls, self-delusions, and the fables, fallacies, and folderol that science generates.
Furthermore, I am inclined to believe that science is not about solutions but about problems and questions, about ignorance rather than knowledge (and that the German adage "Wissenschaft ist was Wissen schaft" is in a fundamental way wrong). That science may sometimes hit or stumble upon a solution for a particular problem is only a fortunate coincidence. The everyday business of science is to generate, test, and possibly reject theories: conjectures and refutations (Popper, 1963).
Before I add yet another misunderstanding, I would like to emphasize that I am skeptical toward all theories. The reader should not be afraid that I shall try to proselytize or impose my own pets upon him. What I intend to do is to present the material as objectively as possible, and everyone should feel absolutely free to reject or accept, or be quite indifferent to, the conclusions I shall eventually draw.

Why, then, one might well ask, embark upon such an enterprise? The answer is, at least part of the answer is, that others have already done so, which gives me an opportunity to weed out the 'just-so stories' from the more compelling arguments. Another partial answer is that this study is also the outcome of an act of faith. If I did not 'believe' at least in the possibility of evolutionary explanation, I would have refrained from it.
It is the belief that evolutionary theory can provide a framework (or paradigm, if one likes) in which social behavior makes more sense in toto than in other

[^2]frameworks (paradigms), or, in other words, that it has potentially greater explanatory power than competing paradigms, in the sense that an evolutionary paradigm can more easily accommodate the other frameworks than vice versa. This is simply another way of stating that an ultimate framework can more easily accommodate proximate frameworks than vice versa (See § 1.2.12).

### 1.1.1 Complications of Culture

The - at least partial - independence of culture, as an 'autonomous' phenomenon, from biological evolution manifests itself, it is argued, at least in three forms or aspects: temporal, spatial and structural. Firstly, the theoretical rate of genetic change in time is too small to meet the rapid changes that have occurred in human cultures historically. Secondly, the very large cultural differences observed among contemporaneous populations cannot be reduced to biological differences. And thirdly, culture is a group phenomenon par excellence, opposed to biological evolution that works through the differential survival and reproduction of individuals.
These differences between biological and cultural evolution have induced social scientists to separate them sharply as independent realities, two distinct domains of human existence. The sociologist Emile Durkheim (1893) stressed that social facts are not reducible to any other level of understanding. Durkheim's legacy has dominated the social sciences during the 20th century. Leslie White (1949) asserted that culture must be considered as a phenomenon sui generis, as a class of events and processes that behaves in terms of its own elements and processes and laws and which, consequently, can be explained only in terms of its own elements, processes and laws. Sahlins (1977) and Sahlins \& Service (1960) regard culture as an arbitrary reality independent from biology. It creates an autonomous symbolic order in a particular society. In this view, human beings are not socially defined by their organic qualities but exclusively by the meaningful values of culture.

In considering warfare from an evolutionarily biological perspective, we implicitly make, of course, the assumption that (aspects of) warring behavior have indeed evolved in the Darwinian sense, and are not just 'cultural inventions'. This is a 'dangerous' assumption for many people, as it seems to imply 'genetic determinism', the worst heresy sociobiology is accused of. Furthermore, such an assumption is quite absurd for those critics, who maintain that human warfare has a history as a one-time cultural invention, but no evolution. Such a position seems implicitly to convey the message that human behavior is totally and absolutely shaped by culture, that human culture has totally and absolutely taken over the hegemony of the genes, and that, hence, any biological approach to human behavior is quite irrelevant.
My first tentative answer to the cultural determinists would be that the discovery of chimpanzee 'warfare', and the growing body of literature on
intergroup conflicts in primates and other mammals (see Ch. 3), make such a monolithically cultural position very unlikely, unless the term culture is substantially diluted.
My second tentative answer would be that all human (and nonhuman) behavior is always the product of complex interactions of many forces or determinants on many levels-of-analysis, including evolutionary ones. Ultimately, all organisms are the products of the former strategies of their genes. And the human being, however magnificent and god-like a creature he may consider himself to be, is no exception.
This is not to deny that the relationship between biological and cultural evolution is still a problematic, controversial, and hotly debated issue. Thus we are informed

- that cultural evolution is just the continuation of natural evolution by other means; in other words, that natural and cultural evolution constitute one single evolutionary process;
- that it is Man's nature to have culture, and that all human behavior is 'mediated' by culture;
- that culture and nature are the arguments in a false dichotomy;
- that natural evolution keeps cultural evolution on a leash by means of epigenetic rules in a gene-culture coevolutionary process;
- that cultural evolution operates in the same way as, or analogous to, natural evolution, by means of blind and random variation and selective retention, but on memes or culturgens as replicators instead of genes;
- that cultural evolution is an independent development beyond Darwinian evolution, having non-Darwinian properties: the so-called Lamarckian inheritance of whatever is considered as a unit of cultural transmission;
- that sociocultural evolution is different from biological evolution in speed, structure and dynamics, but is nevertheless rooted in, and constrained by, the behavioral repertoire resulting from biological evolution;
- that Man genetically tracks his culture;
- that culture is, to all effects, the opposite, or even the denial or transcendence, of nature;
- that there is an inevitable (intrapsychic) conflict between Man's 'nature' and the demands and constraints of his culture; or that Man is torn apart by the clashing forces of his innate schizophysiology; or that there is a lag between the evolution of Man's brain and Man's mind; or that Man is a misfit in his man-made environment (these dualistic views mostly equate Man's nature with dark, irrational, uncontrollable and often destructive, forces or motivations bridled by the rational and constructive superimpositions of culture);
- that culture is the mode of transmission of the total set of artifacts and
mentifacts (ideas; descriptive, evaluative and prescriptive information) which enables Man to shelter and protect himself from nature;
- that Man is a unique and rational being totally divorced from nature because humans have minds, symbolic language, rationality, etc. (which virtually always collapses into the same circular argument);

Notice that many of these views imply that there is a non-sequitur, if not outright conflict, between natural and cultural evolution. One neat example is the 'dual inheritance model' of cultural transmission developed by Boyd \& Richerson (1985). They point out that certain evolutionary forces characteristic of cultural evolution may lead to maladaptive outcomes in terms of genetic fitness. The authors thus explicitly admit the possibility of conflicts between cultural and genetic evolution. Also Campbell (1975) envisaged such a possibility: "For many behavioral dispositions the two systems support each other. For others, the two are in conflict, and curb each other", because the retention system of cultural evolution inevitably "includes a lot of noise, maladaptive mutations and chaff, along with selected kernels of wisdom". Curiously - paradoxically? - it is evolutionary reasoning itself which may predict such a nature-culture clash: "... evolutionary reasoning alerts investigators to the likely prospect that crucial aspects of human symbolic behavior, specifically the enhanced capacities for deception and self-deception, may well engender circumstances that encourage individuals to behave contrary to their material and reproductive self-interest" (Crippen, 1992). Culture, in brief, can not be viewed as a mechanism that invariably contributes to fitness maximization.

Another tentative answer might be: It does not matter how a particular behavior arises, whether by Darwinian selection or by cultural invention. Once in existence, however, it is subject to Selection (natural and cultural selection). If this behavior does not contribute to inclusive fitness in the long run, it will be selected against. If it is a cultural trait that does not, on average, enhance the reproductive success or the survival of the protagonists, it will eventually be substituted by another trait (or the protagonists will go extinct).
Cultural and symbolic capacities, which impose high costs on human organisms in terms of energy, nutrients, and risks of malfunction, would not have been retained by natural selection if they did not confer some degree of selective advantage on their bearers (e.g., Irons, 1979; Lopreato, 1984; Green, 1995).

Graham Richards (1987) has sorted out the various theoretical positions regarding the relative statuses of biological and cultural evolution. Briefly, the main schools include (a) Biological evolution has been totally supplanted by sociocultural evolution; (b) Biological evolution and cultural evolution are aspects of a single evolutionary process; (c) Biological and sociocultural
evolution are fundamentally conflicting; (d) Biological and sociocultural evolution are parallel processes; (e) Sociocultural evolution is subordinated to biological evolution.
Richards' overview and lucid account of the merits and demerits of the theoretical stances is highly recommended ${ }^{4}$.

All in all, one gets the impression that many theorists are extremely unhappy with the notions of culture and cultural evolution. This is no dark mystery if one realizes the astonishing complexities involved for a theory of evolution by means of natural selection. Anticipating the exposition of the concepts of contemporary evolutionary biology in the next section, a brief digression to the founding fathers of evolutionary theory might provide a taste of the struggle with the problems involved.

The human capacity for culture and all that it entails (intelligence, language, morality, altruism, justice, etc.) posed a real and serious problem to the early evolutionists (Cronin, 1991). Alfred Russell Wallace, the co-founder of classical Darwinian evolutionary theory, for example, became more and more convinced that natural selection could not possibly account for our advanced mental attributes and the distinctly human brain. And, what is worse, some of these refined capacities would even have been a downright nuisance and a danger "in the severe struggle he [the savage] has to carry on against nature and his fellow-man" (Wallace, 1891).
Charles Darwin strongly disagreed with this view, as did, initially, Thomas Huxley. Eventually, however, 'Darwin's bulldog' came to believe that human morality must have been the result of cultural evolution only: the struggle for existence in nature, he held, is so profoundly red-in-tooth-and-claw that it would smother a developing morality at birth because morality must necessarily work against nature: "[S]ince law and morals are restraints upon the struggle for existence, the ethical process is in opposition to the principle of the cosmic process [the Hobbesian war of each against all], and tends to the

[^3]suppression of the qualities best fitted for success in that struggle" (Huxley, 1894).

Herbert Spencer, the founding father of Social Darwinism (which we shall encounter later on) argued that the inheritance of acquired characteristics was the only possible evolutionary force responsible for the evolution of human morality. His vision was that the inheritance of acquired characteristics (a theory of evolution associated with the French naturalist Lamarck) would bridge the gap between biological and cultural evolution, forging them into one grand seamless process (Cronin, 1991). In the next section I shall return to some of these issues.

My point of view is that many phenomena surrounding war and warfare, war practices, rituals, motives, etc. cannot be properly understood without the sociocultural context (i.e., the shared set of meanings, ideas, concepts, beliefs, values, assumptions) in the construction of the various social cosmologies. We simply cannot do without cultural categories, as will be exemplified in the discussion of the materialist school and the sociocultural construction of what constitutes a resource (Ch. 5). I regard human beings as shrewd social strategists, clever manipulators, and conscious, intelligent decision-makers in the service of their inclusive fitness, operating within the constraints of their cultural semantics: the signification and interpretative frameworks (the semiotics and ethics) provided by the culture they happen to have been born in. The cultural aspects of human behavior should not, however, be portrayed as disembodied systems of symbolic information, as is commonly done by cultural anthropologists. This is a rather curious stance in light of our knowledge of cultural universals (D. Brown, 1991). It is far more plausible to assume that these cultural universals - including language acquisition and structure, toolmaking, kinship rules and incest avoidance, religion, morality, age- and sex-differentiated roles and statuses, some degree of ethnocentrism and territoriality, etc. - are grounded in universal features of human nature, traits that, in turn, are intimately linked to properties of the human central nervous system. As such, both the capacity for and the expression of cultural behavior may be viewed as products of evolution by means of natural selection (Crippen, 1992).

Yet another tentative answer might be: Basically, both natural and cultural evolution are processes of information transmission. One transmits the information contained in the DNA, the other the information contained in the mind. For example, sex (male/female) is a biological category. Gender (masculine/feminine), on the other hand, is a cultural category, implying norms, standards, values, meanings, and templates or prescriptions of appropriate conduct and role behavior; but ultimately the cultural category of gender does not make any sense without the biological category of sex.
It is often asserted that culture is a Lamarckian process. It means that social
knowledge and organization are transmitted not by genes but by learning, from simple imitation to linguistic information. The function of culture is to transmit the information acquired during individual life from generation to generation. In this sense culture really is a Lamarckian process that departs radically from biological evolution in both structure and dynamics.
However, culture may conform to the Darwinian 'logic' in at least three different senses. Firstly, the biological capacity for culture itself is transmitted genetically. Secondly, sociocultural traits still cannot escape ultimate evolution by natural selection. Finally, cultural evolution could follow the same laws and principles that work in biological evolution.
The core of the sociobiological approach is that behavioral capacities and tendencies have developed in response to the environment in human evolutionary history through natural selection. Human customs, social institutions and cultural forms have not developed in a biological vacuum, but under the conditions of interactions with natural selection. The biological nature of early Homo must have faced the ecological challenges in the ancient environment, have influenced the elementary shapes of social structures, and have constrained possible trajectories of human history.

### 1.2 The Concepts of Evolutionary Theory

In the following paragraphs, the instrumentarium (the conceptual apparatus and basic ideas) of neo-Darwinian evolutionary biology will be briefly introduced. A thorough understanding of the basics of sociobiology is indispensable in order to grasp and appreciate the explanatory power of the evolutionary framework.

### 1.2.1 Evolution by Means of Natural Selection

According to Mayr (1982), the classical theory of evolution by means of natural selection consists of three inferences based on five facts. The first inference claims that since more individuals are produced than can be supported by available resources, there must be a fierce struggle for existence among the individuals of a population, resulting in the survival of only some of the progeny of each generation. This inference is based on the facts that (1) all species have great potential fertility (fecundity), (2) populations normally display stability, and (3) natural resources are limited and, in a stable environment, remain relatively constant.
The second inference claims that survival in the struggle for existence is not random but depends in part on the hereditary constitution of the surviving individuals. This unequal survival constitutes a process of natural selection. This inference is based on the facts that (4) no two individuals are exactly the
same and (5) that much of this variation is heritable.
The third inference claims that over the generations this process of natural selection will lead to a continuing gradual change in populations, that is, to evolution and the production of new species (speciation).

Note that this formulation of classical Darwinian theory is still considered to be valid, though much of the terminology has now changed (e.g., 'competition for scarce resources' versus 'struggle for existence'; 'reproductive success' versus 'fitness'), and the modern (also called 'synthetic') theory of evolution is thoroughly gene-centered instead of organism- or group-centered as it was in Darwin's time.
In contrast to classical Darwinism, the emphasis now is not on morphology and anatomy of organisms, but on behavior - or more accurately, on behavioral strategies; and not on survival or differential mortality, but on differential reproductive success as the only currency in the cold calculus of evolution. In order to reproduce at all, an organism has, of course, to survive at least till the age of sexual maturity in the arena of nutritional competition, before it can enter the arena of reproductive competition.

From this account of evolution by natural selection, it may be deduced that selection is both short-sightedly opportunistic and conservative. Conservative in the sense that it does not create ex nihilo, but by remodeling, reshaping, retinkering, or 'refunctioning' whatever happens to be available of existing structures, substrates and behavior. That is why many of our organs give the strong impression of being provisional patchwork (which, by the way, is not the only reason: they are often also uneasy compromises as a result of different, conflicting, opposing and mutually counteracting, selection pressures). Adaptive organization, as Pittendrigh (1958) stated, is "a patchwork of makeshifts pieced together, as it were, from what was available when opportunity knocked, and accepted in the hindsight, not the foresight, of natural selection". And not only a 'patchwork of makeshifts', but also a 'tangle of compromises' (Tinbergen, 1965). Like a river, natural selection blindly meanders its way down along the successive trajectories of immediately available least resistance.
In classical theory, it was little appreciated that substantial costs are involved: Every evolutionary adaptation must cost something, costs being measured in lost opportunities to do other things. There are always costs and trade-offs involved (Dawkins, 1982; Cronin, 1991).
And evolution is short-sightedly opportunistic in the sense that there is no ulterior goal, no 'Grand Design of Nature', no 'Plan of Progress', no 'Point Omega'. Whatever is momentaneously and selfishly beneficial, i.e., whatever contributes to an individual's reproductive success (and that is what 'fitness' is all about) will be selected for, even if that what is selected for is to the detriment of the species as a whole. This latter statement may come as an
unpleasant surprise to those readers who are accustomed to think that organisms happily, harmoniously, and even self-sacrificingly, cooperate and reproduce in order to ensure the survival and secure the continuation of the species.
Another principle eminently enters the stage as soon as this harmonious and erroneous view of nature is abandoned. Having limited time and energy budgets, and basically needing the same, and equally limited, resources and commodities for survival and reproduction as their conspecifics, organisms may be expected to compete with, and be in conflict with one another more or less continuously and ubiquitously, and to have developed neurophysiological, endocrinological and behavioral structures and mechanisms adapted to such situations of competition and conflict, at least in primordial form. And because, as evolutionary biology furthermore predicts, in sexually reproducing species one sex (mostly the males) competes for the ultimately limiting reproductive resource (mostly the females), armaments, vigor and fighting capabilities are in many species confined to, or more developed and conspicuous in, the males. Agonistic behavior and its morphological paraphernalia are almost universally sexually dimorphic.
In this view, organisms are clever and shrewd - though not necessarily conscious - strategists and inclusive fitness maximizers (which is expected to be reflected in the 'software' of the individual, i.e., its motivational, emotional and cognitive make-up).

### 1.2.2 Competition and Conflict

Conflict on all levels of organic existence is pervasive, persistent, ubiquitous. Conflict is the universal experience of all life forms. Organisms are bound in multiple conflict-configurations and -coalitions, which have their own dynamic and their own logic. This does not mean, however, that the more paroxysmal forms of conflict behavior, naked violence and destruction, are also universal. Conflict and cooperation are always intertwined. Conflicts do, however, have a propensity to gravitate towards violence.
Sociobiological reasoning predicts conflict potentials in every area where there is a relative difference in coefficients of relatedness, and wherever the reproductive interests of individuals are not absolutely identical: motherembryo conflict, parent-offspring conflict, sibling rivalry, conflict between the sexes (the 'battle of the sexes'), male-male conflict, female-female conflict, and intergroup conflict along ethnic, 'racial', tribal, ideological and other boundaries and cleavages.
Indeed, field observations of a great number of species have confirmed these predictions: feticide, infanticide, siblicide, homicide, cannibalism and kronism, and rape, as the most extreme and gory forms of 'conflict-resolution', are much more widespread in the animal kingdom than was ever envisaged by the first generation of ethologists, such as Lorenz, who thought that animals had innate
inhibitions against killing conspecifics, and that Homo sapiens sapiens was a biological freak and misfit because he apparently lacked those inhibitions ${ }^{5}$.
But, as will be seen, competition and conflict do not, automatically and inevitably, imply violence. Violence - the elimination, destruction, incapacitation or mutilation of the opponent - is one way to attempt to (re)solve conflict, and very often it is not the most sensible way, as it incurs extremely high costs (in terms of the time and energy budget: wasted time and opportunities, exhaustion, and injuries or death) to the organism that engages in such behaviors, and the benefits to be derived do not often exceed the costs (bear in mind that even superficial wounds and lacerations make the animal vulnerable to sepsis, infection and debilitation or death). In contrast to the vision of nature as 'red-in-tooth-and-claw' (Tennyson), which suggests violence, destruction, bloodshed, cruelty and callousness, contemporary evolutionary biology does not stipulate that violence is the best strategy. It does not, however, exclude the possibility in certain well-defined circumstances either (See § 1.3.1).

The universality and ubiquity of conflict in the animal and the human world is, in evolutionary-biological theorizing, expected on the basis of competition over scarce or limiting resources. The units which compete for these scarce resources can be individuals, coalitions of individuals, populations (interdemic competition), species (interspecific competition), etc.
Theoretically, populations of two species may interact in 9 basic ways: neutralism, mutual inhibition, competition, amensalism, parasitism, predation, commensalism, proto-cooperation, and mutualism (Odum, 1971; E.O. Wilson, 1975). Interspecific competition, or competition of two species for the same resources is, as E.O. Wilson $(1970$, 1975) explains, more fatal than a predator-prey relation. Competition eventually leads to the extermination of the species with the smaller growth capacity; a predator-prey relation only leads to periodic oscillation around a mean value (Volterra, 1928; von Bertalanffy, 1968).

Competition, as Miller (1967) modified the original Clements \& Shelford (1939) definition, is "the active demand by two or more individuals of the same

[^4]species (intraspecies competition) or members of two or more species at the same trophic level (interspecies competition) for a common resource or requirement that is actually or potentially limiting". This definition is consistent with the assumptions of the Lotka-Volterra equations, which still form the basis of the mathematical theory of competition (Levins, 1968).
Intraspecific competition occurs when two or more individuals seek access to a resource that is somehow important to the fitness of each and that is restricted in abundance such that optimal utilization of the resource by one individual requires that another settle for suboptimal utilization. In other words, if there is enough to go around, then there is no reason for competition - e.g., few animals ever compete for air. However, severe competition may erupt over food, water, nesting sites, and/or appropriate mates (Barash, 1977, 1979; Cf. E.O.Wilson, 1970, 1975; Daly \& Wilson, 1978; Trivers, 1985; Huntingford \& Turner, 1987; Archer, 1988; van der Dennen \& Falger, 1990; van der Dennen, 1992; a.o.).
Nicholson (1955) was the first to make a distinction between contest competition and scramble competition. Non-aggressive scramble competition occurs when each participant attempts to accumulate and/or utilize as much of the critical resource as it can, without regard to any particular social interaction with its competitors (comparable to an Easter egg hunt). If the resource is used up in the process, then the winners of scramble competition are the individuals who have converted the largest part of that resource into copies of themselves. Fitness in this case has been achieved by simply out-reproducing the competition, usually by being most efficient at locating, exploiting, or garnering the resource in question.
In contrast, contest competition would be occurring if the participants first argued, fought, or somehow disputed among themselves, and then use the outcome of such interactions to determine access to resources: To the victor belong the spoils (Barash, 1977; Huntingford \& Turner, 1987).
The fitness of both parties (that is their chances of surviving and reproducing) will depend critically on how these conflicts are resolved. So we should expect to find that animals have evolved ways of increasing their chances of coming out on top. Alternatively, competition may be sidestepped by mutual avoidance, either in space or in time.

Responses to conflicting interests other than scramble competition are often referred to as interference competition. The use of physical coercion in response to a conflict of interest is often described as aggression. Aggression may be considered to be the proximate mechanism of contest competition. It takes place when individuals interact with each other such that one of them is induced to surrender access to some resource important to its fitness. The exact forms of aggression vary widely, from intimidating displays and threats to actual fights. It may be considered to be a special case of coercive manipulation in which the desired outcome is brought about by intense displays, which can, if required, be escalated to direct physical confrontation,
and injury, or even death, of one or both of the contestants (Barash, 1977; Huntingford \& Turner, 1987). Just as animals are expected to exert themselves to acquire important resources or enlarge their supply, thereby enhancing their fitness, they are also expected to resist the loss of important resources, thereby avoiding decrements to their fitness.
Offense is often differentiated from defense in both human and animal conflict behavior. It is hard to draw a clear dividing line at any point of the continuum from offense or attack through offensive and defensive threat and submission to escape, yet it seems improper to include escape under the heading of aggression. Therefore 'agonistic behavior' (from the Greek $\alpha \gamma \omega Y$ meaning 'contest'), which refers to a "system of behavior patterns having the common function of adaptation to situations involving physical conflict" (Scott \& Fredericson, 1951), is offered as the more inclusive term.

Another (and independent) distinction is that made by E.O. Wilson (1975) between resource competition (called 'nutritional competition' by Symons [1979]) and sexual competition (called 'reproductive competition' by Symons). Sexual competition involves access to receptive mates; it may include both contest and scramble forms. One form of sexual competition which is similar to scramble competition is unobtrusive mating (or kleptogamy), where a male sneaks up to one of a number of females which are being guarded by another male.
There are a number of indirect forms of sexual competition which fall into the category of 'contest' competition yet do not involve fighting. In males, competition may take the form of removing a rival's sperm prior to mating, sperm competition, or olfactorily induced pregnancy block. In females, it may take the form of suppression of the reproductive activity of other females (e.g., Archer, 1988).

The evolutionary rules underlying interspecific variations in competitive aggression specifically for food resources have been covered by J.L. Brown (1964), E.O. Wilson (1975), Clutton-Brock \& Harvey (1976), Geist (1978), and Archer (1988) among others. When food is abundant, aggression will be unnecessary since the same benefits can be obtained without it. When food is scarce, it will often be advantageous for the animal to use its energy in foraging for food (i.e., scramble competition) rather than in contest competition, particularly when food is widely dispersed or difficult to find. In general, therefore, we might expect aggression to occur under conditions of intermediate food availability.

### 1.2.3 Selfish Gene Theory

One of the greatest achievements of evolutionary biology is perhaps its ability to explain the apparent harmony, beauty, peacefulness, cooperation and altruism that we undoubtedly perceive in much of nature as outcomes of individual, self-centered and short-sighted conflict strategies (or, rather, the strategies of the genes of which the individual is just the temporary vehicle).
Though already suggested some 50 years ago by mathematically oriented biologists like Fisher (1930) and Haldane (1932), it has only very recently been realized that the basic unit of natural selection is not the species, the group, the individual, or even the chromosome: it is the formerly hypothetical (and potentially immortal) gene. It consists of desoxyribonucleic acid (DNA), and its most important biochemical property is its tendency to make replicas or copies of itself. As Dawkins (1976) in his anthropomorphic metaphor puts it, each gene 'selfishly' attempts to spread as many copies of itself as possible. This copies-maximizing behavior is the result of natural selection, genetic variation, and, ultimately, the biochemical properties of the DNA. In this parlance, also, the individual organisms are merely the vehicles or throw-away survival machines for those selfish genes (Dawkins, 1976 et seq.; Wind, 1982 et seq.; Cronin, 1991).
Interestingly, we may expect conflict even at this level of 'selfish' genes: Intragenomic conflict. There are now known, for example, to be genes causing segregation distortion ('meiotic drive') which makes them to be present in more than half of the gametes. As G.C. Williams (1979) made clear: "The really fundamental question in evolution may be answerable only by regarding each gene as ultimately in conflict with every other gene, even those at other loci in the same cell" (Cf. Crow, 1979; Cosmides \& Tooby, 1981; Dawkins, 1982; Wind, 1984; and Ridley, 1993).

### 1.2.4 Game Theory and the Concept of 'Evolutionarily Stable Strategy' (ESS)

Natural selection is ultimately differential survival of alleles in gene pools. We can talk about the Darwinian evolution of behavior only if we are prepared to visualize genetically determined behavioral alternatives in the population. Each genetically determined behavioral alternative is referred to as a 'strategy'. A strategy in this sense can be defined only by contrast with at least one alternative. It does not have to be something the animal works out in a cognitive or purposive sense. Rational decisions do not come into ESS theory. Rather, each organism is assumed to be provided with a nervous system which is wired up in advance so that it performs in a certain way, programmed, in other words. A strategy stands to an organism in the same relation as a program to a computer. It is an unconscious behavior program, a candidate for natural selection in competition with alternative strategies. Then we can ask which program or combination of programs will be stable against evolutionary invasion by alternative minority programs which might arise in the population by mutation or immigration (Maynard Smith, 1974, 1976, 1978; Maynard Smith \& Price, 1973; Maynard Smith \& Parker, 1976; Dawkins, 1980; Caryl, 1981)

The defining characteristic of an ESS, according to Dawkins (1980), is not that it is the optimum or even the 'best' strategy for all individuals involved. Rather, it is immune to cheating. In simpler phrasing, an ESS is a strategy with the property that if most of the members of a large population adopt it, then no mutant strategy can invade the population. In other words, a strategy is evolutionarily stable if there is no mutant strategy that gives higher Darwinian fitness to the individuals adopting it. Any mutants practicing a different strategy will reap a lower reproductive payoff, and eventually will die out (Maynard Smith, 1978) ${ }^{6}$.
In § 1.3 the concepts of strategy and ESS will be applied to a game-theoretical analysis of (the evolution of) ritualized or conventional aggression.

[^5]
### 1.2.5 Group Selection

Group selection is one of the most confused and confusing topics in modern evolutionary biology. It is part of an ongoing and sometimes acrimonious, controversy over the 'level-of-selection'. The term 'group selection' is used in a dazzling number of different meanings. One generic meaning of the term 'group selection' is the idea that a trait may evolve for the benefit or the 'greater good' of the group or species, but at the expense of the individual gene carrier. In brief the group selection paradigm states that 'something' evolves because it is good, or beneficial, or advantageous, or functional, or adaptive for the group or the species. A recurrent problem with the group selection paradigm is that 'something' (be it somatic or behavioral) which evolves for the good of the individual organism always overrules that which may evolve for the 'greater good' of the species. One example may suffice to illustrate this important principle of evolutionary biology: Induced abortions, intrauterine resorption of embryos, cannibalism and kronism of offspring, nest desertion and infanticide exist as evolved mechanisms and behaviors (strategies, for short) in many species. These strategies can hardly be construed as good for the (preservation of the) species. Yet, they have evolved, and virtually all of these strategies can be shown to be adaptive in terms of reproductive success, not for the species but for the individual organism practicing them.
Claims that selection operates at a higher level than the individual, that is, at the level of the group or species, favoring traits that allow these larger units to survive, have been variously called the 'group selection fallacy', the 'species benefit fallacy' or 'greater goodism'.
This idea of 'greater goodism', as will be seen, is now commonly rejected for reasons elaborated below, and, as Maxwell (1991) explains: "Within sociobiological circles, belief in this phenomenon marks you as a member of the out-group. The theory of group selection is viewed as one of the great mistakes made by earlier biologists - notably by Wynne-Edwards (1962). It holds that traits (particularly altruistic traits) that make Group A more fit than Group B (as a group) can proliferate because Group A will survive and Group B will die out. For instance, a group or population of animals that limits its birthrate would avoid overconsumption of resources and consequent famine, hence it would do better than a groups of prolific profligate individuals. The flaw in group-selectionist thinking is that there is no way to explain how the early mutants with this self-sacrificing trait would survive - they would obviously be out-reproduced by their fellow groupmembers. For the most part, it has now been shown (by George C. Williams [1966] and others) that the illusion of group selection can usually be explained by individual selection or by kin selection".
The mechanisms involved are quite easy to understand: "Traits that lower individual reproductive success tend automatically to be eliminated from the
population so that later, possible indirect benefits to the species itself are irrelevant to the traits' fate within the species. All traits must begin as rare in a species and can increase in frequency only if they increase the survival and reproductivity of those bearing the traits" (Trivers, 1985)
But there is a more fundamental reason why group selection, in this sense, is evolutionarily very unlikely, and that is the basic difference between replicators and vehicles (See § 1.2.9).

The other generic meaning of the term 'group selection' is the idea that in the course of human evolution, groups have competed with one another - some groups subjugating other groups, some groups absorbing and assimilating other groups, some groups even eliminating other groups altogether - and that these events must have had an impact on the gene pools and (the direction of) human evolution. As applied to the human species, therefore, group selection may be eminently possible, "since one group of humans can consciously organize their altruistic behaviors and wipe out a rival group" (Maxwell, 1991). We shall encounter especially this latter meaning of 'group selection' in the chapters to follow.
This latter meaning of the term 'group selection' is probably what Darwin envisaged when attempting to explain human morality (which posed a serious problem for his theory). Darwin starts by considering competition between groups. If a group that has a high proportion of unselfishly devoted members comes into conflict with a group that has a high proportion of selfish members, it is easy to see that the group of altruists will triumph. Their discipline, fidelity, courage and other such qualities will soon ensure victory. But the problem is to explain how unselfishness ever got off the ground in the first place: "[H]ow within the limits of the same tribe did a large number of members first become endowed with these social and moral qualities, and how was the standard of excellence raised?" (Darwin, 1871). Unselfish members would not have the most offspring, Darwin realized - quite the contrary:

It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those which were the most faithful to their comrades, would be reared in greater number than the children of selfish and treacherous parents of the same tribe. He who was ready to sacrifice his life... rather than betray his comrades, would often leave no offspring to inherit his noble nature. The bravest men, who were always willing to come to the front in war, and who freely risked their lives for others, would on an average perish in larger number than other men (Darwin, 1871).

He concedes that the problem looks almost intractable: "Therefore it seems scarcely possible... that the number of men gifted with such virtues, or that the standard of their excellence, could be increased through natural selection, that
is, by the survival of the fittest". Darwin sees two ways out of the difficulty. One is reciprocity: "[E]ach man would soon learn that if he aided his fellowmen, he would commonly receive aid in return". But when he turns to his other solution, he seems to suggest that individual sacrifice for the sake of the group can evolve because it pays off in intergroup competition:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection (Darwin, 1871).

This passage, as Cronin (1991) comments, is puzzling. Darwin specifically said that he is now tackling the problem how altruism gets established within the group; he takes care to remind us "that we are not here speaking of one tribe being victorious over another". And yet he seems to be speaking of exactly that.

See Grafen (1984), Melotti (1987) and Cronin (1991) for a host of other meanings of the term 'group selection'. To confuse matters more, it must be admitted that E.O. Wilson, the founding father of sociobiology, did not reject group selection as a theoretical possibility. He argued that "pure kin and pure interdemic selection are the two poles at the end of a gradient of selection on ever enlarging nested sets of related individuals" (E.O. Wilson, 1975).
Alexander (1974), another 'ancestor' of modern evolutionary biology, even reasoned that especially human groups would be expected to have been amenable to powerful group selection:

For two reasons human social groups represent an almost ideal model for potent selection at the group level. First, the human species is (and possibly always has been) composed of competing and essentially hostile groups that frequently have not only behaved toward one another in the manner of different species, but also have been able quickly to develop enormous differences in reproductive and competitive ability because of cultural innovation and its cumulative effects. Second, human groups are uniquely able to plan and act as units, to look ahead and purposely carry out actions designed to sustain the group and improve its competitive position. These features may actually represent an exhaustive list of the precise attributes of a species that would maximize its likelihood of
significant group selection, or evolution by differential extinction of groups. Thus group selection involves the paradox that competing populations must be sufficiently isolated to become different in ways that may lead to their differential extinction yet close enough together that they can replace one another. This condition is obviously fulfilled with sympatric competing species, which are intrinsically isolated. So, to some extent, are hostile neighboring populations of humans (Alexander, 1974).

To confuse matters even more, if that is still possible, cultural anthropologists use the term 'group selection' or 'cultural selection' (vide infra) in their own idiosyncratic way, sometimes contrasting it with 'biological group selection', sometimes contrasting it with 'biological selection', and sometimes simply referring to group competition. I warned you it was a confusing topic.

### 1.2.6 Cost/Benefit Calculus and 'Good-for-the-Species' Thinking

Even without a sophisticated ESS analysis it is not difficult for a modern Darwinian to see that a male animal might well do better by showing some restraint in combat with other males:

After all, a policy of let-rip could be very costly. Even a strong male in his prime could have a lot to lose. Opportunity costs, for example: time and energy that he devotes to vanquishing rivals cannot be devoted to catching prey or attracting mates (aggressive neglect). And then there is the fact that, however useful it is to have a rival out of the way, it is equally useful for his other rivals, and it is he that has paid the removal costs. What is more, if the animal that he is fighting already possesses the mate or territory that he wants, the possessor was presumably once a victor, so he is challenging a former champion. In short, the benefits must be set against the costs. Darwin, Wallace and their contemporaries failed to see the costs of conventions. Failing to see the costs of combat is just another side of that same coin (Cronin, 1991).

Gradually, as 'good-for-the-species' thinking began to permeate Darwinism, conventional combat shed its visibility. "Ritualization... has been very important" Julian Huxley stated "in reducing intra-specific damage, by ensuring that threat can ensure victory without actual fighting, or by ritualizing combat itself into what Lorenz calls a tournament... [T]ournament fights provide maximum damage-reduction" (Huxley, 1967).

Indeed, ritualized combat came to play a starring role in greater-goodism. What better evidence that natural selection works for the good of the species than that two hefty rivals, capable of tearing one another limb from limb, choose to settle matters peaceably, with a nod and a grunt?

This line of thinking culminated in the 1960s with Konrad Lorenz's book On Aggression (1966). "Though occasionally, in territorial or rival fights, by some mishap a horn may penetrate an eye or a tooth an artery, we have never found that the aim of aggression was the extermination of fellowmembers of the species concerned" (Lorenz, 1966, p. 38). By contrast, aggression towards other species is no-holds-barred. Or so, at least, Lorenz seems at times to be telling us. And he has certainly been widely criticised for taking a group- or species-level view (e.g. Ghiselin, 1974; Kummer, 1978; Maynard Smith, 1972; Ruse, 1979). Lorenz's Darwinism is so confused, however, that it is impossible to tell what exactly he had in mind.
It is to Wynne-Edwards that one must turn both for an explicit recognition that conventional combat poses a problem and for an explicit attempt to explain it by group selection:
"[T]he wholesale wounding and killing of members by one another is generally damaging to the group and has consequently been suppressed by natural selection... [A]ny immediate advantage accruing to the individual by killing and thus disposing of his rivals for ever must in the long run be overridden by the prejudicial effect of continuous bloodshed on the survival of the group as a whole... [C]onventions... have evolved to safeguard the general welfare and survival of the society, especially against the antisocial, subversive self-advancement of the individual" (Wynne-Edwards, 1962, pp. 130-1).
At least one knows where he stands, even if it is resolutely in the wrong place. 'Preservation of the species' has no evolutionary relevance whatsoever, even though, of course, the interests of the individuals and the interests of the group or species do seem to coincide neatly and seamlessly (Cronin, 1991).

In this study, evolutionary theory serves a twofold purpose. Firstly, it serves as a kind of selection criterion (no pun intended): In analogy to Occam's razor it may be called Darwin's scissors. Theories and hypotheses about human behavior, especially war and warlike activities, that do not incorporate some biologic or actually run counter to selection thinking are considered to be not very viable in the long run. The alternative would inevitably boil down to the assertion that the behavior concerned is some arbitrary, random, senseless and purposeless 'cultural whim', to be 'explained' by an equally arbitrary and capricious 'cultural theory'. To be sure, many human behaviors are rather arbitrary and senseless, and to be understood in their historical and cultural context, but regarding matters of life and death, of survival and procreation, of sex and violence, war and peace, this is unlikely to be the whole story. Especially in these vital and lethal domains of life the strategies of the genes can be expected to be prominently and abundantly present.
And secondly, selection thinking provides a basis for comparing species as
strategists: Other organisms have had to solve the same kinds of problems as we had: problems of uneasy coexistence, of sociality and competition, predation, parasitism, mate selection, parental investment, exploitation and manipulation, etc. Comparing species as strategists also avoids the common and presumptuous - fallacy of speciesism or anthropocentric apartheid: The, mostly implicit, assumption that all non-human animals (from bacteria to chimpanzees) fall into one single explanatory category whereas Homo $s$. sapiens alone stands apart, an entirely different explanatory realm.

Now, that assumption really is mistaken - and speciesist to boot. There are many, many ways of being a Darwinian strategist. And they don't divide neatly into 'human ways' and 'all the rest'. The reason that we are justified in assuming sameness of strategic principles is that, although behaviour is manifested in organisms, strategies belong ultimately to genes. And genes are not speciesist.
What is more, to erect a biological apartheid of 'us' and 'them' is to cut ourselves off from a potentially useful source of explanatory principles. Once we have understood ourselves as naturally selected tacticians, we might have a suggestive heuristic guide to the tactics that natural selection has employed with other living things...
All we need to imagine is that, in pursuit of the same strategies as ours, other living organisms might have converged on the same tactics. There's nothing unduly anthropomorphic about that. We're not assuming that organisms think as we do. We're not even assuming that they think at all. After all, chromosomes and plants manage to implement Darwinian principles even without brains. It is natural selection that has done their 'thinking'. Nevertheless, their strategic choices and ours could run parallel, the structure of their behaviour could be the same, because natural selection has implemented its strategies in similar style. Admittedly, we are unique. But there's nothing unique about being unique. Every species is in its own way (Cronin, 1991).

### 1.2.7 Kin Selection and Inclusive Fitness

Besides Selfish Gene Theory and ESS, the third basic idea of sociobiology (and the one which triggered its origin) is the explanation of the paradoxical behavior which (somewhat anthropomorphically) is called altruism: why should an individual organism decrease its fitness or even sacrifice itself for another individual? Many individuals among the social insects, for example, do not reproduce and even sacrifice themselves for their conspecifics (See Ch. 3). Indeed, as Cronin (1991) observes, in some respects animals behave more like the moral paragons of Aesop - working dutifully for the sake of the community, noble in spirit and generous in deed - than the hard-bitten, selfseeking individualists that relentless natural selection would seem to favor.

The answer is that their genetic relationship is such that decreasing their own fitness, or even reducing it to zero, may contribute to the survival of the copies of the individual's genes present in other individuals. This is most apparent in its kin, and this type of selection is therefore called kin selection: the fitness of the individual and that of its relatives sharing the same genes is called inclusive fitness. More formally, we can speak of a gene's effect on an individual's inclusive fitness: the amount by which the gene increases or decreases the reproductive success of the individual, plus the amount by which it increases or decreases the reproductive success of relatives, each amount weighed by the appropriate degree of relatedness (On the concept of inclusive fitness see especially: Fisher, 1930; Haldane, 1932; Hamilton, 1963 et seq.; E.O. Wilson, 1975; Dawkins, 1976, 1979, 1985; Van den Berghe \& Barash, 1977; Michod, 1982; Krebs \& Davies, 1984; Grafen, 1984; Trivers, 1985; Fox, 1989; Cronin, 1991) ${ }^{7}$.

In order to appreciate this solution, consider for a moment what exactly, and how enormous, the problem was for the Darwinian view of nature. I freely paraphrase Cronin's (1991) eloquent account:

A bird gives an alarm call. This seems a highly altruistic act: warning others of danger but perilously alerting predators to its own presence. How can we explain it? If we take an organism-centered view, as did classical Darwinism,

[^6]we simply shall not be able to. Worse, if we take a group- or species-level view, we might be able to 'explain' it all too easily as for the 'greater good' of the group or species. And we shall end up in the kind of muddle that permeated Darwinism for several decades. But what if we hold steadily to a gene-centered view?
If the beneficiaries of the altruistic act are the animal's relatives, we can explain it by kin selection theory: Natural selection would favor saving my kin rather than my skin, if the aid would be differentially and discriminatingly targeted toward members of my family. It is not easy for a gene to 'recognize' copies of itself in other individuals, but the rules to discriminate between kin and nonkin need not require brothers and sisters and nieces and nephews to be identified as such. They could be very simple indeed: 'Help those reared in the same nest as yourself' or 'Help those with the same smell as yourself' or (in altricial species) 'Help your neighbor' (See also Ch. 7).

But what if the beneficiaries of the altruistic act are not the animal's kin? How might we explain altruistic behavior then? Reciprocity (if you scratch my back, I'll scratch yours'), first suggested by Trivers (1971, 1985), is one answer. What looks like altruism might really pay the participants: they could be exchanging altruistic favors in such a way that each does better from cooperating than it would from failing to cooperate. The costs of a good deed are compensated for by a good deed in return. But how could such a mutually beneficial arrangement come about? To a selfish Darwinian strategist it is ripe for exploitation. Certainly, cooperation pays. But would not defecting pay the defector even more? Far from evolving, the cooperation would degenerate into cheating, with defectors seizing unrequited good turns. If only everyone would cooperate, everyone would be better off; but the best course for any individual is to pursue its own self-interest; and so everyone will inevitably end up worse off: The perennial 'tragedy of the commons'.
Axelrod \& Hamilton (1981) and Axelrod (1984) turned to a well-analyzed model in game theory, the Prisoner's Dilemma, because it captures just that problem: The rational pursuit of individual self-interest driving everyone into an outcome that nobody prefers.

But the dilemma has a solution. Suppose that the participants play the game repeatedly, suppose that each knows that the two of them are likely to meet an indefinite number of times. Under such conditions cooperation can evolve. Consider, for example, the strategy Tit for Tat: cooperate on the first move and after that copy what the other player did on the previous move. Tit for Tat is never the first to defect; it retaliates against defection by defecting on the next move but subsequently lets bygones be bygones. It turns out that this highly cooperative strategy can evolve, even when initially pitted against exploitative, readily-defecting strategies. And it can be stable against invasion by them. If it is to get off the ground, a
critical proportion of its encounters must be with cooperators like itself; otherwise the strategy Always Defect will evolve and be stable instead. In short, Tit for Tat pretty well amounts to an evolutionarily stable strategy (ESS): once it, or something very like it, exceeds a critical frequency in the population, then such a strategy will be stable against invasion from any other.
In evolution, a strategy is represented in any generation in proportion to its success in the previous generation. So, the more a Tit-for-Tat-like strategy is successful, the more likely it will be to encounter itself and the more it will be able to reap the rewards of mutual cooperation. And so it is that out of Darwinian self-interest cooperation can evolve; out of selfishness comes forth altruism (Cronin, 1991).

Reciprocal altruism ${ }^{8}$, as an exchange of mutually beneficial favors, is in fact not 'altruism' in the high-strung colloquial meaning of the word, but plain vanilla genetic self-interest, as is kin altruism. As a relatively complex form of social behavior, reciprocal altruism may be expected to be highly developed in our own species, as it necessitates individual recognition and memory, cost/benefit calculations, and the ability to detect, and take appropriate action against, cheaters (non-reciprocators). Trivers (1971) uses the term 'moralistic aggression' to characterize the commonly punitive action against cheaters.
As will be seen later on, the lex talionis, the uncodified law of the eye-for-aneye revenge, may be viewed as a kind of negative 'reciprocal altruism' or reciprocity for short: "I render onto you in exact return the evil you have inflicted upon me or my kin". Vengeance and retaliation in 'primitive' societies are, to a large extent, based on notions of equity, fairness, distributive justice, and moral obligation.

[^7]
### 1.2.8 Exploitative Manipulation and Evolutionary Arms Races

Cooperative altruism does not exhaust the possibilities to explain the behavior of the vigilant bird. We have always to keep in mind that the behavior is really utterly selfish. As suggested by Zahavi (1977, 1987), who studied this sentinel behavior in a fascinating bird species, the Arabian babbler, living in Israel's Negev semi-desert, the sentinel is doing so to help itself - and because of the danger. It is as if the babbler were communicating to its companions: "Look at what I can manage. I am strong and robust and alert enough to bear the burden of sentinel duty, to take on the costs and still be able to thrive. Only an individual of high quality could afford to handicap itself so much". So babblers positively compete to replace other group members as sentinels. There can be substantial benefits - especially in status position - to showing-off this way, even though it may impose severe costs.

Let us return once again to the bird that gives an alarm call, but now suppose that it is a fake alarm call, that the bird is actually manipulating its fellow conspecifics. It is plainly 'whistling a lie'; there is no imminent danger of raptors or other predators. It just wants the others out of the way, fleeing to safety, in order to feast on some tidbits itself, undisturbed by its rivals. Such faking behavior has indeed been observed in birds (e.g., Munn, 1986). But then immediately the question arises: Why do these other birds let themselves be duped? The answer probably lies in an asymmetry in the selective forces: The useful gains from occasional cheating versus the possibly fatal danger of not taking every alarm call at face value.

Finally, we must consider the possibility that the behavior really is selfsacrificial, that of a victim, a pawn, the instrument of others. This possibility derives more or less logically from 'extended phenotype thinking' (Dawkins, 1982): One organism subtly and exploitatively manipulating another to the manipulator's advantage. Perhaps some altruists really are acting against their own best interests, under the influence of genes that are in another organism's body.
Consider a cuckoo's unwitting hosts, sacrificing themselves and their own offspring to satisfy their demanding foster-child. We could look on their behavior merely as a mistake, a ready-made niche that the cuckoo is using for its own ends rather than the ends 'intended' by natural selection. On this analysis, the cuckoo's behavior is explained adaptively but the hosts' is not.

We could, however, look on the behavior of the hosts as an adaptation, but this time as an adaptation that benefits the cuckoos, the adaptive phenotypic effect of a manipulative gene in the cuckoo's body. On this analysis, too, there could be an arms race, with the hosts struggling to take
more control of their own destiny and the cuckoos tightening their grip or moving on to easier prey.
There may well be an asymmetry in the strength of the selective forces acting on the cuckoos and their hosts. On the hosts' side, it may not be worth the costs to invest in counter-adaptations against manipulation; spending a season rearing a cuckoo need not be fatal to reproductive success and might anyway be a rare event for any individual member of the host species. By contrast, we can expect the cuckoos to put up an impressive evolutionary fight because for them this race is a matter of life and death (Cronin, 1991).

So the cuckoos probably owe some of their victory to the 'life-dinner principle': "The rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner" (Dawkins, 1982).
The life-dinner principle' illustrates a more general point about arms races and manipulation. If there is any asymmetry in the strength of the selective forces acting on the two sides, if the forces affecting the manipulator are more critical, more stringent than those affecting the manipulated, then natural selection will be unlikely to rescue the exploited from their exploitation. "If the individual manipulator has more to lose by failing to manipulate than the individual victim has to lose by failing to resist manipulation, we should expect to see successful manipulation in nature. We should expect to see animals working in the interests of other animals' genes" (Dawkins, 1982).

I have dwelt on these subjects of manipulation and exploitation not only because they illustrate most ingeniously the subtleties of evolutionary thinking, but also because it has become increasingly clear that these mechanisms exist indeed, are alive and kicking - in the social behavior of many species including, and especially, Homo s. sapiens. 'Genteel' ideas of some vaguely benevolent mutual cooperation in social relationships are gradually being replaced by an expectation of stark, ruthless, opportunistic mutually exploitative manipulation (Alexander, 1974 et seq.; Ghiselin, 1974; Dawkins \& Krebs, 1978; Dawkins, 1982; Trivers, 1985), especially within the family, in the 'battle of the sexes' (van der Dennen, 1992), and, most pertinently, in the context of intragroup cooperation for intergroup competition, and the uneasy human intergroup relations themselves.

### 1.2.9 Replicators and Vehicles

Rather than reviewing the many criticisms of higher-level selection, it is more illuminating to clarify the logic behind it all, which rests on the fundamental distinction between replicators and vehicles (Dawkins, 1976 et seq.).
Only genes possess the biochemical properties to be replicators: They reproduce copies of themselves, on the whole faithfully, but with occasional
'translation errors' (mutations); and they have phenotypic effects that influence the gene's fate. So natural selection can act at the level of genes; genes are the only serious candidates for units of selection, not individual organisms, and not demes, groups, populations, species, etc.
But if organisms are not replicators, what are they? The answer is that they are vehicles of replicators, carriers of genes, instruments of replicator preservation, temporary throw-away 'life support systems' and 'survival kits'. Replicators are what get preserved by natural selection; vehicles are means for this preservation. Organisms are well integrated, coherent, discrete vehicles for the genes that they house; but they are not replicators, not even crude, low-fidelity replicators.
Similar considerations hold, though even more strongly, for groups and other higher levels. Although in some loose sense they renew themselves, divide, bud off, persist, nevertheless they cannot be true replicators. They have no reliable means of self-propagation (Cronin, 1991).
Selection is differential survival, and the units that survive over evolutionary time are not groups or individuals but replicators. Only genes are potentially 'immortal'.


#### Abstract

What light does all this throw on adaptations? Adaptations must be for the good of replicators, for the good of genes. But they are manifested in vehicles. Genes confer on vehicles properties that influence their own replication. So adaptations could, in principle, turn up at any level - at the level of organisms (either in the organism that bears the gene or in another), at the level of groups and even higher. There is no rigid rule as to where they will be manifested, in which vehicle (nor how). They are, however, most likely to occur in the organism that bears the gene. This is not only because the closest vehicle is the most amenable to physical influence. It is also because genes that share a body are likely, to a large extent, to 'agree' over which phenotypic effects are adaptive. Conflicts of interests among same-body genes are dampened down by a common interest in the survival and reproduction of that body. Any gene in a genome will have been selected, among other things, for its compatibility with other genes in that genome, its contribution to their joint endeavour. And yet warring factions can arise even among genes that share a body. So how much more likely, and how much more acute, conflicts of interest will be among the looser assemblages of genes that make up higher-level vehicles - groups, populations, species (Cronin, 1991).


### 1.2.10 Adaptations and Adaptiveness

Basically, an adaptation is a tentative solution to recurrent evolutionary problems. An adaptation is an anatomical structure, physiological process, or behavior pattern that enabled ancestral organisms to survive and reproduce in competition with other members of their species (G.C. Williams, 1966). Behavioral adaptations often involve behaviors that are contingent on conditions in the environment (and may even be sexually dimorphic). Hence, they may not appear to be characteristic of all members of the species. Crawford (1991) distinguishes two types: concurrently contingent strategies, and developmentally contingent strategies. Behavioral adaptations often provide alternative behaviors that depend upon either concurrent or past environmental conditions. It is the whole repertoire of behaviors that is considered to be adaptive, or at least has been adaptive in the past.
It should be realized that not all behavior and other - morphological or physiological - properties (or traits) are necessarily adaptive ${ }^{9}$ or contributory to spreading gene copies. The individual can be considered as a compromise of many different, competing - but necessarily cooperating - genes and hence organs or organ systems.
Adaptation is the change of gene frequencies as a result of new (re)combinations and of changing ecological pressures resulting in a new ESS. Such a change implies time-inertia, i.e., many generations (Wind, 1984). But even given sufficient time to a species, not every one of its individuals can be expected to be optimally adapted; theoretically, only one genotype would be, and absence of genetic variability is nonadaptive. Finally, of course, behavior adaptive in one situation may be nonadaptive in another situation. Or rather, as van der Steen \& Voorzanger (1985) have pointed out: behaviors can never be adaptive, full stop. Behavior A may be adaptive in comparison with behavior B, but nonadaptive in comparison with behavior C. In situational terms this must be translated as: Behavior A may be adaptive in comparison with behavior B in situation X, neutral in comparison with behavior C in situation X , and nonadaptive in comparison with behavior D in situation X , in which X is almost infinite.

In a recent report on the Human Behavior \& Evolution Conference, Glantz (1989) noticed a basic controversy which divided the Behavioral Ecologists and the Evolutionary Psychologists. The basic point of disagreement was this: Is current human behavior adaptive (i.e., does it function to maximize inclusive fitness), and related to this, is the brain a general purpose processor or does it

[^8]possess domain-specific mechanisms (i.e., modularity)?
If the brain is set up as a general purpose processor, it can work just as well in all kinds of environments, ancestral as well as contemporary, so it can be expected to produce adaptive behavior in all kinds of environments. The brain, in this perspective, is a great big machine that is designed to take all inputs, whatever they might be, and find the solution that maximizes inclusive fitness. If, on the other hand, the brain has special-purpose sub-processors (domainspecific modules) that are designed to deal with specific types of problems, it is likely to do much better in some environments (those where such problems are crucial) than in others (i.e., those where new kinds of problems have arisen).
"You need the general purpose hypothesis in order to assert that behavior is always adaptive, even outside the natural environment. You don't need it if you believe that behavior is sometimes adaptive and sometimes not" (Glantz, 1989).

Is it necessary for evolutionists to prove that people today are maximizing their fitness, Glantz wonders, and he provides the answer that it is enough to show the continuing effect of adaptive mechanisms created by natural selection sometime in the past, continuing to exert some influence over current behavior. "I think that the difference between the two positions can be illustrated by two versions of the 'central theorem' of sociobiology. The standard version reads as follows: "On the average, all organisms act in such a way as to maximize their inclusive fitness". The EP version might read: "On the average, all organisms have mechanisms which cause them to act in such a way as to maximize inclusive fitness as long as they are living in their Environment of Evolutionary Adaptedness (EEA). Outside of EEA, the mechanisms may or may not produce adaptive behavior".

### 1.2.11 ESS versus EQUUS

Like any branch of science, sociobiology has its limitations (Wind, 1982 et seq.). There are two main reasons why sociobiology should not be expected to provide easy answers to the intricacies of human social behavior. One reason is inherent in the discipline, as Wind (1984) explains: "While the basic paradigm of sociobiology - the selfish-gene concept - is quite simple as well as scientifically quite valid, the difficulties in its application in behavioral analyses seem to increase exponentially when passing from viroids and viruses (in which genotype and phenotype are virtually identical) and unicellular organisms to simple multicellular ones and the higher vertebrates including man. In the same order the practical value of sociobiology decreases".
The other reason is more intricate and substantial. It has become increasingly clear that Homo s. sapiens, no longer the 'Crown of Creation' ever since Darwin, is indeed an exceptional and odd species in the world of organisms. The time elapsed since our origin is - in evolutionary perspective - quite brief. Therefore, many of our genes' frequencies and behaviors are still oscillating
without having reached yet a less disequilibrated state as is usually found among other - 'older' - species. Stated in less technical terms, we are still in the wake of our evolutionary origin. Enigmatically, H. s. sapiens often seems to show evolutionarily odd properties such as celibacy, contraception, abortion, infanticide and other nonreproductive or even counter-reproductive behaviors. In other words, human beings do not seem to be intrinsically motivated to invariably maximize the number of their offspring.
Hence, properties or traits - behavioral, physiological, or morphological - may exist that do not contribute to the spreading of gene copies, or that even hamper it, though, admittedly, these properties are likely to occur much less frequently than those that do contribute to fitness.
Some of these odd properties may, in fact, very well have, at the individuals' level, a negative selective value, and may be in the process of being selected against. Such a process will last longer when that negative selective value is smaller. Finally, odd behavior may be the result of recurrent mutations, pleiotropy, linkage and other genetical mechanisms.
Because of these reasons $H$. s. sapiens is likely to show behaviors that can sociobiologically be qualified as an Evolutionarily Quite Uncommon, Unstable Strategy (EQUUS), instead of an Evolutionarily Stable Strategy (ESS) (Wind, 1982 et seq.) ${ }^{10}$.

### 1.2.12 Ultimate versus Proximate Explanations

An important distinction in evolutionary biology, indeed in any attempt to explain animal and human behavior, is that between ultimate (or evolutionary or phylogenetic) and proximate (or immediate or ontogenetic) causes.
A proximate explanation considers the immediate causation of that behavior in psychological or neurophysiological terms (e.g., stimulus configurations, motivations, appetites, physiological homeostasis, hormonal priming, dispositions, drives, etc.), or - on a larger time scale - in ontogenetic terms (e.g., growth, development, maturation, acquisition, learning, conditioning, habit formation, scenarios, scripts, social roles, etc.). But the time scale involved in proximate explanations is confined to the life span of the individual, from embryo in utero to corpse in humero.
An ultimate explanation, on the other hand, would ask: why did this particular behavior evolve? Did it confer fitness advantages in the past to the bearer of this particular set of genes?

[^9]Many critics of sociobiology and, indeed, many sociobiologists themselves often fail to distinguish these levels-of-explanation. The proximate cause of a primitive raid may be, for example, the seeking of revenge, the redressing of a perceived evil to the ingroup. An ultimate approach would address the question how and why in (vertebrate?, primate?, hominoid?, human?) phylogeny revenge warfare ever developed: why was it selected?, had it survival value?, did it contribute to inclusive fitness?, did it lead to greater reproductive success in those species or peoples who practiced it than in those species or peoples that did not have it in their behavioral repertoire?
These and similar questions invoke the time scale of evolution, of phylogeny, of the millions of years of natural selection that shaped us into what we are today.
"Natural selection can honestly be described as a process for the maximization of short-sighted selfishness" as G.C. Williams (1988) states, but as the principle of kin-selection suggests, we are equally selected to be (short-sighted or not) nepotistically altruistic. Natural selection operates through the differential reproductive success of individual members of a population (or rather their genomes: the strategies of their selfish genes, of which the individual is just the temporary vehicle). We may expect that those genes that have not 'programmed' their temporary vehicles with strong urges to reproduce have been selected against since time immemorial.
We may also expect all organisms, including our own species, to be programmed to compete for differential reproductive success with their conspecifics, and for the resources and status positions which lead to the enhancement of reproductive success. But because our next-of-kin also bear replicas or copies of our own genes, natural selection will also favor those behavioral strategies which increase the reproductive success of our next-ofkin. This is 'kin-selection', and it is measured in terms of 'inclusive fitness', and its manifestation is nepotism or nepotistic altruism. A particular behavior is 'adaptive' only in so far as it contributes to the organism's inclusive fitness. It is rather easy to see that the concept of 'preservation of the species' has no evolutionary relevance whatsoever. Reproductive success of the individual organism is the only currency in the calculus of evolution.
Kin-selection also implies that the competing social units during human evolution were kinship clans, and that, as Chagnon (1988) states: "in the tribal world warfare is ipso facto the extension of kinship obligations by violence because the political system is organized by kinship".

### 1.3 The Evolution of (Ritualized) Aggression

The concept of aggression as the proximate mechanism of contest competition was originally proposed by Barash (1977), and in this evolutionary context it is a very useful one.
There is much in favor of viewing a great deal of animal behavior as optimum strategies for maximizing the rate of extraction of 'fitness gain' from the available series of 'fitness gain parameters' (resources) present in its environment. One consequence of the occurrence of discontinuously distributed resources is that they may be in short supply. Animal aggression (in the form of resource guarding) will be favored by selection when there are less resources than competitors and where an individual can achieve an immediate gain in fitness by forcibly ousting one of its conspecifics.
Selection for aggression will be more intense the more discrete the resource (i.e., the easier it is to guard) and the higher its yield as a fitness gain parameter (a function both of its absolute effect and its shortness of supply).
It is not surprising therefore that most of animal aggression relates to food fighting and especially to mating. Territoriality (vide infra) is often merely an adjunct to these two situations - an area is guarded because it has a high probable yield of food or mates, or both (Parker, 1974; Cf. Barash, 1982).
Aggression is expected to be modulated by the degree of relatedness of the competing individuals (Hamilton, 1964). Darwin (1871) was very well aware of the individual advantages of aggression when he founded the theory of sexual selection.

Animals invest time and energy in agonistic behavior and can run serious risks of injury or even death from fighting. Injury and death are obvious risks of fighting but displays and fights can also expose an animal to predators. Apart from the risk of attracting predators, males on lekking grounds run the risk of losing body condition or even starving because of the need to stay on the territory and keep displaying.
Observations from the field and data on the bioenergetic costs of combat, of living subordinate to a victor, of healing wounds, of the shorter life expectancy as a consequence of higher susceptibility to predation when wounded, of the loss of mating opportunities (aggressive neglect), the cost of gaining access to resources to restore dominance, and of the chance to kill or injure kin, suggest that combat as an activity, and its consequences, are very expensive indeed. As well as the costs, however, there are also substantial benefits to being aggressive. Individuals can thereby gain exclusive use of a resource such as a food source, or may win exclusive mating rights. The more aggressive an animal is, the more benefits it may gain (such as extra food). But if an animal is too aggressive it might face unacceptably high costs (such as serious injury) so
the animal must weigh up the relative costs and benefits of its action and choose an optimum level of aggression (i.e., maximize the net benefits). If the costs are too high and the benefits too low, avoiding a fight may be preferable to competing. In other cases it may be worthwhile to fight vigorously, even to risk death, for a big enough prize, e.g., a mating opportunity.

It is evident that there is value in searching for alternatives to combat that have much the same ultimate effects but not the same consequences. It has been recognized repeatedly that threats and displays probably evolved to substitute for combat (Collias, 1944; Walther, 1958 et seq.; Geist, 1966 et seq.; Schaller, 1967; a.o.).
Threats are iconic signals clearly directed at an individual indicating incipient attack. (Dominance) displays, on the other hand, are abstract signals from which one cannot predict the actor's action. They appear to aim at arousal by generating uncertainty in an opponent by emphasizing the size of weapons or body. The displayer does not address the opponent directly, and often changes his movements from the normal to act exaggeratedly slow or fast.
Of the two, threats are probably the more expensive since they gear up the individual physiologically for combat, and they increase the risk - and hence the consequences - of a counterattack by the threatened opponent. We can therefore assume that combat elements are most costly, since they do lead to visible exertion of the opponents, threats are next in costliness, and dominance displays are least costly per display (Geist, 1978).
Fear may represent psychophysiologically the more or less realistic assessment of the costs of an agonistic interaction.

In its application to the analysis of the evolution of agonistic behavior, game theory assumes that behavior has costs (ranging from death or serious injury to exhaustion or mere waste of time) and benefits (acquisition of a food item, a potential territory, or a mate) which can be quantified in units based on the contribution to the individual's reproductive fitness (Caryl, 1981). A useful discussion of the reasons for the choice of this unit as a 'common currency' is presented by McCleery (1978).
The game-theoretical models also include assumptions about strategies (or tactics, or gambits) that an individual is allowed to adopt in a dispute, and about the chances of victory, or of incurring costs, while using these tactics. The benefits that accrue to an individual adopting particular tactics will depend on what tactics are adopted by other members of the population, and for some models, this frequency dependence leads to perpetual change in the proportion of individuals adopting particular tactics (Caryl, 1981).
Maynard Smith \& Price (1973) were the first to propose a model of the evolution of conflict behavior in which selection acts entirely at the individual level, but in which the success of any particular strategy depends on what strategies are adopted by other members of the population.

### 1.3.1 Ritualized Aggression

The power of the concept of the Evolutionarily Stable Strategy, and other concepts discussed above, can be illustrated by its application to the puzzling phenomenon of ritualized combat, or conventional aggression, between individual conspecifics. I freely adopt and adapt Cronin's (1991) account.

Combat between individual male conspecifics can be very dangerous, even lethal, especially in the mating season, as Darwin (1871) already noticed. But ritualized fighting is no myth, as Darwin noticed too.
Evolutionarily, ritualized fighting poses a considerable theoretical difficulty, as pointed out by E.O. Wilson (1975) and Dawkins (1976): Why not always try to kill or maim the enemy outright? And when an opponent is beaten in a ritual encounter, why not go ahead and kill him then? Why not deliver the final coup de grâce whenever the situation permits? Why do animals hold back when they could slaughter, and eliminate the competitor once and for all? Allowed to run away, to paraphrase the childhood rhyme, the opponent may live to fight another day - and win next time. So in a sense the kindness shown an enemy seems altruistic, an unnecessary risk of personal fitness.
If everyone else is foolish enough to obey such rules, why do not individuals break them, bluffing and cheating or going all-out for a quick victory?
For the Lorenzian school of ethology ritualized aggression was no problem at all. On the contrary, it was evidently and 'naturally' for the preservation of the species. Such 'good-for-the-species' arguments are no longer tenable, however, and we have to look for an explanation at the genic level.
ESS theory suggests that it is not enough to snatch a quick victory in a single encounter. What matters is whether a strategy is evolutionarily stable. Any strategy that is successful will end up, over evolutionary time, encountering itself more than it encounters any other strategy. So if it is to be evolutionarily stable against invasion, it must be able to do better against itself than any other strategy does against it:

We must think, then, not just about a single encounter, nor even about all of a male's encounters over his lifetime, but about the career of a strategy over evolutionary time. From that perspective, things begin to look different.
Imagine a pugnacious bully, throwing his weight about, always ready for fight, always ready to pursue it to the bitter end. His rival is a coward, sloping off at the first sign of trouble, avoiding a punch-up at all costs. The bully will clearly do better in any particular encounter. But is bullying likely to be evolutionarily stable? Remember that we are not talking about a particular bullying individual. We are talking about a strategy acting out its bullying role in many different individuals over many generations.

Successful strategies will come to be represented in the population in proportion to their success. So eventually any bully will encounter other bullies more often than he encounters cowards. And when the bullying strategy encounters itself, costs will be greater and victory less assured. Bullying may no longer pay.
We can see, then, that a strategy of all-out fighting for instant gains may well not be evolutionarily stable. And we can begin to see why, under a range of conditions, conventional combat may well be (Cronin, 1991).

To return to Wilson's (1975) question "Why do animals prefer pacifism and bluff to escalated fighting?", several lines of evidence suggest that non-lethal patterns of settling disputes, such as agonistic displays that end short of fighting, ritualized combat, and submission and appeasement signals, have most likely evolved because such behaviors benefit the individual actors engaging in these behaviors, not because species preservation calls for such beneficial patterns of behavior. In other words, individual animals generally do not kill or seriously wound conspecifics because usually it is not in their own genetic self-interest to do so (Fry, 1980).
The main conclusion reached by pioneers Maynard Smith \& Price (1973) was that in a species capable either of 'ritualized' or 'escalated' fighting - the latter being capable of seriously injuring an opponent - the evolutionarily stable strategy is to adopt the ritualized level, but to respond to escalation from an opponent by escalating in return. In a population adopting such a 'retaliation’ strategy, a mutant which adopted escalation tactics too readily would be more likely to get seriously injured than the typical members of the population, who would usually settle conflicts without escalation.
If one views the various types of ritualized aggressive behavior witnessed in many species as reflections of individuals generally pursuing evolutionarily stable strategies, then overly pugnacious animals (as well as too zealous pacifists) would appear to be penalized in terms of reproductive success and fitness. In many circumstances, actors that fight more frequently or more forcefully than the majority of their conspecifics normally do would stand a higher chance of serious injury than their less pugnacious peers. If for instance an overly aggressive fighter continues a struggle with an already submissive partner, the latter, acting out of self-defense, may in turn escalate its response and seriously injure the imprudent opponent (Fry, 1980).

Maynard Smith (1974) distinguished two types of ritualized contest: tournaments' and 'displays'. An example of a tournament is a fight between two male deer, in which the antlers interlock and a pushing match ensues. The structure of antlers and the behavior of the contestants is adapted to prevent serious injury. Physical contact does take place, however, and victory usually goes to the larger, stronger and healthier individuals.
Tournaments of this kind are common. In such cases, no special difficulty
arises in understanding how a ritualized contest can be settled; the model considered by Maynard Smith \& Price (1973) seems adequate to explain why more dangerous weapons or tactics do not evolve.
In a 'display', no physical contact takes place, or if it does so it does not settle the contest and provides little or no information about which contestant would win an escalated contest. In such a contest, the winner is the contestant who continues for longer, and the loser the one who first gives way. It is the logic of contests of this kind (the so-called 'War of Attrition') that is considered by Maynard Smith (1974).

### 1.3.2 A Simple Model: The War of Attrition

The War of Attrition is one of the simplest models that have been considered. It represents a contest which is settled by display alone. In the model, individuals are imagined to show their threat display at constant intensity until one gives up, leaving the other, which was prepared to go on at this point, as the winner.
In this game Maynard Smith (1974) showed that the ESS is to choose the duration of the display, X , according to the negative exponential distribution

$$
\mathrm{P}(\mathrm{X})=(1 / \mathrm{V}) \exp (-\mathrm{X} / \mathrm{V})
$$

The average cost of the contest (owing to the time wasted in the display) under this model is equal to $\mathrm{V} / 2$, where V is the gain from victory (Maynard Smith, 1974).

There exists a single ESS for most War of Attrition models with a monotonous increase of costs during attrition, and that is to settle the conflict according to 'who has more to gain or less to pay for persistence' (Hammerstein \& Parker, 1982).

The War of Attrition is an example of an important class of models that Caryl (1981) calls 'continuous models'; the cost of a contest, dependent on its duration, is continuously variable. An alternative type of model is what Caryl calls the 'discrete model'. In this model, the contest can be fought at two distinct levels of escalation, and the most important factor in bringing it to an end is serious injury, which produces a large, discrete, increment in the cost of the contest and causes the injured animal to cease fighting. Game theorists have used discrete models to model escalation in animal contests, assuming that the escalation involves a series of steplike changes in the intensity and potential danger of the interactions (Caryl, 1981).

### 1.3.3 Hawks and Doves

The simplest discrete model is the famous Hawks and Doves game (Maynard Smith, 1976; Maynard Smith \& Parker, 1976). The pay-off matrix is shown in Fig. 1.3.3.

|  | Hawk | Dove |
| :---: | :---: | :---: |
| Hawk | (V-D) $/ 2$ | V |
| Dove | 0 | $\mathrm{~V} / 2$ |

Fig. 1.3.3. The Hawks and Doves game. The payoffs in the table are to the tactic in the row when played against the column. V is the gain from victory, D the cost of injury. For the matrix shown, which ignores the cost of threat, the ESS is to escalate with probability $\mathrm{P}=\mathrm{V} / \mathrm{D}$ (when V < D). If threat imposes a cost T on each opponent, the probability of escalation becomes $\mathrm{P}=(\mathrm{V}+2 \mathrm{~T}) /(\mathrm{D}+2 \mathrm{~T})(\mathrm{Caryl}, 1981)$.

Consider this simple model: A (theoretical) species that in contests between two individuals has only two possible tactics, a 'hawk' tactic and a 'dove' one. A hawk fights without regard to any convention and escalates the fighting until it either wins (that is, until its opponent runs away or is seriously injured) or is itself seriously injured. A dove never escalates; it fights conventionally, and then if its opponent escalates, it runs away before it is injured.
At the end of a contest each contestant receives a payoff. The expected payoff to individual X in a contest with individual Y is written $\mathrm{E}(\mathrm{X}, \mathrm{Y})$. The payoff is a measure of a change in the fitness of X as a result of the contest, and so it is determined by three factors: the advantage of winning, the disadvantage of being seriously injured and the disadvantage of wasting time and energy in a long contest. For the hawk-dove game suppose the effect on individual fitness is +10 for winning a contest and -20 for suffering serious injury. Suppose further two doves can eventually settle a contest but only after a long time and at a cost of -3. (The exact values of the payoffs do not affect the results of the model as long as the absolute, or unsigned numerical, value of injury is greater than that of victory).
The game can be analyzed as follows. If the two individuals in a contest both adopt dove tactics, then since doves do not escalate, there is no possibility of injury and the contest will be a long one. Each contestant has an equal chance of winning, and so the expected payoff to one of the doves D equals the probability of D winning the contest $(\mathrm{p}=1 / 2)$ times the value of victory plus the cost of a long battle, that is, $\mathrm{E}(\mathrm{D}, \mathrm{D})$ equals $(1 / 2)(+10)+(-3)$, or +2 .
Similarly, a hawk fighting another hawk has equal chances of winning or being injured but in any case the contest will be settled fairly quickly. Hence the
expected payoff $\mathrm{E}(\mathrm{H}, \mathrm{H})$ is equal to $(1 / 2)(+10)+(1 / 2)(-20)$ or -5 . A dove fighting a hawk will flee when the hawk escalates, so that the dove's expected payoff is 0 and the victorious hawk's payoff is +10 .
Now suppose the members of a population engage in contests in the hawkdove game in random pairs and subsequently each individual reproduces its kind (individuals employing the same strategy) in proportion to the payoff it has accumulated. If there is an ESS for the game, the population will evolve toward it. The question, then, is: Is there an ESS for the hawk-dove game? It is evident that consistently playing hawk is not an ESS: a population of hawks would not be safe against all mutant strategies. Remember that in a hawk population the expected payoff per contest to a hawk $\mathrm{E}(\mathrm{H}, \mathrm{H})$ is -5 but the expected payoff to a dove mutant $\mathrm{E}(\mathrm{D}, \mathrm{H})$ is 0 . Hence dove mutants would reproduce more often than hawks. A similar argument shows that consistently playing dove is also not an ESS.

Serious injury $=-20 \mathrm{E}(\mathrm{H}, \mathrm{H})=1 / 2(+10)+1 / 2(-20)=-5$
Victory $=+10 \quad \mathrm{E}(\mathrm{H}, \mathrm{D})=+10$
Long contest $=-3 \quad \mathrm{E}(\mathrm{D}, \mathrm{H})=0$
$\mathrm{E}(\mathrm{D}, \mathrm{D})=1 / 2(+10)+(-3)=+2$

|  | Hawk (H) | Dove (D) |
| :---: | :---: | :---: |
| Hawk $(\mathrm{H})$ | -5 | +10 |
| Dove | 0 | +2 |

There is, however, a mixed strategy that fulfils the requirements of an ESS. A mixed strategy is one that prescribes different tactics to be followed in a game according to a specified probability distribution. The mixed strategy that is evolutionarily stable for the hawk-dove game is play hawk with probability $8 / 13$ and play dove with probability $5 / 13$. The hawk-dove model predicts that mixed strategies will be found in real animal contests, either in the form of different animals adopting different tactics (such as hawk and dove) or in the form of individuals varying their tactics (Maynard Smith, 1978).
If the cost of injury D is so great that it exceeds the value of the prize, V , then hawks cannot exclude doves from the population: the ESS is a mixed equilibrium with $\mathrm{p}=\mathrm{V} / \mathrm{D}$ where p is the proportion of hawks. If $\mathrm{D}<$ or equal V then all animals are hawks (Caryl, 1981).
Treisman \& Collins (1980) demonstrated that in addition to the value of the prize and the possible damage inflicted, the animal's fitness prior to a contest may affect the ESS for that contest in the hawk-dove game.

### 1.3.4 The Prudent Hawk Gambit

It could be argued that display only rarely involves a high cost, whereas this is required in every escalated contest. But suppose a new gambit arose which involved escalating to the same level as hawks, but withdrawing after a suitable period of time even if no injury had occurred. The principle involved could be the same as that which allows animals to decide when to terminate display, and the period could be adjusted so that the occasional serious injury produced an average cost of V/2. Caryl (1981) calls this gambit the Prudent Hawk. This is the payoff matrix for the Prudent Hawk game:

|  | Hawk | Prudent Hawk | Dove |
| :---: | :---: | :---: | :---: |
| Hawk | $(\mathrm{V}-\mathrm{D}) / 2$ | $-((\mathrm{V}-\mathrm{D}) / 2) . \mathrm{V} / \mathrm{D}$ | V |
| Prudent Hawk | $((\mathrm{V}-\mathrm{D}) / 2) . \mathrm{V} / \mathrm{D}$ | 0 | V |
| Dove | 0 | 0 | $\mathrm{~V} / 2$ |

To give the doves a chance, Caryl reverts to the convention that threat carries no cost. The new gambit would always win over doves; it would also sometimes win over hawks, although it would sometimes be injured in these contests. When the probability of injury in contest between two prudent hawks is V/D (so that the cost of these contests is equal to their average payoff, V/2), the ratios of types are:

| Hawks | Prudent Hawks | Doves |  |
| :--- | :--- | :---: | :---: |
| $1 /(\alpha-1)$ | $:$ | 1 | $:$ | $1 / \alpha$

where $\alpha=\mathrm{D} / \mathrm{V}$, the 'riskiness' of escalating. When $\alpha=2$, hawks and prudent hawks each form $40 \%$ of the population, but when $\alpha=8$, prudent hawks have risen to $79 \%$. Thus by escalating, but stopping when prudent, an individual can do very well, and under this model most combats should be escalated.
However, few should lead to serious injury - most would stop before this occurs. Intuitively, this seems to fit the biological facts better than the original model in which all escalated contests ended in serious injury. Geist's (1971) review of data on moose and other species showed that it involved risk of injury or death (respectively) of about $10 \%$ and $4 \%$ per year, not per contest, while data for mule deer give an estimate of $10 \%$ per year as the chance of injury (Geist, 1974), and data for musk oxen give values of $5 \%$ to $10 \%$ per year for the chance of death (Wilkinson \& Shank, 1976).

### 1.3.5 Pure, Mixed, and Conditional Strategies

Hawk and dove are pure strategies. But 'play hawk with probability $p$ ' is a mixed strategy, and so is 'wait for a time $t$ where $t$ is drawn at random from a probability density function'. The diagnostic feature of a mixed strategy is that its specification contains at least one probabilistic statement ('Stochastic' might be a better label than 'mixed').
The mathematical equivalent of a mixed strategy can be achieved if each individual plays a pure strategy, the population as a whole containing a mixture of pure strategists. We can thus think of the hawk-dove game as ending in a stable polymorphism, a mixture of pure hawks and pure doves in critical proportion, $p$.
But equivalently the ESS could consist in each individual being a stochastic dawk, choosing to play dove or hawk at random, with a built-in bias corresponding to the critical proportion, $p$. Any combination of these two extremes would be stable, provided that in the population as a whole the strategy hawk was played $p$ of the time and dove $1-p$ of the time (Dawkins, 1980).

A conditional strategy is like a computer program with an 'IF' statement, such as 'retaliate IF your opponent attacks you'. Maynard Smith \& Parker (1976) have considered the often surprising consequences of postulating strategies conditional upon asymmetries in aggressive contest between two individuals, for instance, 'attack if larger, retreat if smaller'(Vide infra).
In mammalian species where dominant males hold harems of females, subordinate males sometimes adopt a strategy known as kleptogamy (CluttonBrock, Albon \& Guinness, 1979; Cox \& LeBoeuf, 1977). Kleptogamists sneak briefly into harems and steal hurried copulations before being chased away by the harem master. It is possible that in some species kleptogamy and haremholding genuinely represent two strategies in a stable mix. In this case the average benefit of the two strategies will be equal.
But in most cases it is much more likely that harem masters fare consistently better than kleptogamists, and that the ESS is the pure conditional strategy: 'if possible hold a harem; if not, be a kleptogamist'. Then in the stable state all males will be playing this one strategy, and the behavior that an individual actually shows will be conditional on factors such as his size or skill in combat (Dawkins, 1980).

### 1.3.6 Asymmetric Contests

It is obvious that real animals can adopt strategies that are more complex than 'Always escalate', 'Always display' or some mixture of the two. For example, some animals make probes, or trial escalations. Other employ conventional tactics but will escalate in retaliation for an opponent's escalation. There is, however, another important way in which many real animal contests do not conform to the hawk-dove model. Most real contests are asymmetric in that, unlike hawks and doves, the contestants differ from each other in some area besides strategy. Three basic types of asymmetries are encountered in animal contests.
First, there are asymmetries in the fighting ability (the size, strength or weapons) of the contestants: Differences of this kind are likely to affect the outcome of an escalated fight.
Second there are asymmetries in the value to the contestants of the resource being competed for (as in a contest over food between a hungry individual and a well-fed one): Differences of this kind are likely to affect the payoffs of a contest.
Third, there are asymmetries that are called uncorrelated because they affect neither the outcome of escalation nor the payoffs of a contest. The uncorrelated asymmetries are of special interest because they often serve to settle contests conventionally (Maynard Smith, 1978; Cf. Maynard Smith, 1974; 1976; Parker, 1974; Maynard Smith \& Parker, 1976; Parker \& Rubenstein, 1981; Cronin, 1991). Nature offers asymmetries in abundance.
Perhaps the best example of an uncorrelated asymmetry is found in a contest over a resource between the 'owner' of the resource and an interloper. In calling this an uncorrelated asymmetry it is not meant that ownership never alters the outcome of escalation or the payoffs of contests; it simply means that ownership will serve to settle contests even when it does not alter those factors. To demonstrate the effect of such an uncorrelated asymmetry Maynard Smith (1978) returns to the hawk-dove game and adds to it a third strategy called bourgeois: If the individual is the owner of the resource in question, it adopts the hawk tactic; otherwise it adopts the dove tactic.
In this game it is assumed that each contest is between an owner and an interloper, that each individual is equally likely to be in either role and that each individual knows which role it is playing. The payoffs for contests involving hawks and doves are unchanged by the addition of the new strategy, but additional payoffs must be calculated for contests that involve bourgeois contestants. For example, in a contest between a bourgeois and a hawk there is an equal chance that the bourgeois will be the owner (and so playing hawk) or the interloper (and so playing dove); hence $\mathrm{E}(\mathrm{B}, \mathrm{H})$ equals $1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{H})+$ $1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{H})$ or -2.5 . The remaining payoffs are calculated in a similar manner.

Fig. 1.3.6. The Hawk-Dove-Bourgeois Game
Serious Injury $=-20$
Victory $=+10$
Long Contest $=-3$

$$
\begin{aligned}
& \mathrm{E}(\mathrm{H}, \mathrm{~B})=1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{H})+1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{D})=-5 / 2+10 / 2=+2.5 \\
& \mathrm{E}(\mathrm{D}, \mathrm{~B})=1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{H})+1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{D})=+0+2 / 2=+1 \\
& \mathrm{E}(\mathrm{~B}, \mathrm{H})=1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{H})+1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{H})=-5 / 2+0=-2.5 \\
& \mathrm{E}(\mathrm{~B}, \mathrm{D})=1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{D})+1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{D})=+10 / 2+2 / 2=+6 \\
& \mathrm{E}(\mathrm{~B}, \mathrm{~B})=1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{D})+1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{H})=+10 / 2+0=+5
\end{aligned}
$$

|  | Hawk (H) | Dove (D) | Bourgeois (B) |
| :---: | :---: | :---: | :---: |
| Hawk (H) | -5 | +10 | $+2^{1 / 2}$ |
| Dove (D) | 0 | +2 | +1 |
| Bourgeois (B) | $-2^{1 / 2}$ | +6 | +5 |

The main point, however, is that there can never be an escalated contest between two opponents playing bourgeois, because if one is the owner and playing hawk, then the other is the interloper and playing dove. Therefore the payoff $\mathrm{E}(\mathrm{B}, \mathrm{B})$ is equal to $1 / 2 \mathrm{E}(\mathrm{H}, \mathrm{D})+1 / 2 \mathrm{E}(\mathrm{D}, \mathrm{H})$, or 5 . When this figure is compared with the other payoffs, it is not difficult to see that consistently playing bourgeois is the only ESS for this game. Thus ownership is taken as a conventional cue for settling contests (Maynard Smith, 1978).
In biological terms, a method for settling contests by taking into account some asymmetric feature, such as first arrival on a territory, which could not by itself influence the outcome, can be evolutionarily stable.

### 1.3.7 Conventional Fighting as Assessment of Resource Holding Power (RHP)

Parker (1974; Cf. Parker \& Rubenstein, 1981) examined the view that the adaptive value of conventional aspects of fighting behavior is for assessment of relative Resource Holding Power (RHP) of the combatants. According to this view, outcome of aggressive disputes should be decided by each individual's fitness budget available for expenditure during a fight (determined by the fitness difference between adoption of alternative strategies, escalation or withdrawal without escalation) and on the rate of expenditure of the fitness budget if escalation occurs (determined by the RHPs of the combatants).
Thus response thresholds for alternative strategies ('assessments') will be
determined by natural selection on a basis of which opponent is likely to expend its fitness budget first, should escalation occur. This 'loser' should retreat (before escalation) and the winner should stay in possession of the resource.
Many aggressive decisions depend on whether one is a resource holder, or an attacker. Assuming the RHP of the combatants to be equal, there are many instances of fitness payoff imbalances between holder and attacker which should weight the dispute outcome in favor of one or other opponent by allowing it a greater expendable fitness budget.
Usually the weighting favors the holder; the attacker therefore needs a correspondingly higher RHP before it may be expected to win.
According to Parker (1974), there seems little doubt from the literature that assessment of RHP is occurring in most cases of animal combat. To avoid any implications of teleology, it must be stated that 'assessment' in this context means only that the individual responds differentially to opponents on a basis of their RHP relative to its own; the only assessment of what is the appropriate response is the unconscious one performed by selection.
Size, strength, weaponry, and experience all seem involved in RHP. Males are usually dominant over females. This often relates to RHP disparity because males are bigger; in some instances however secondary sexual characters are used as signals, e.g., comb size is a determinant of dominance in chickens (Collias, 1943). It seems possible that because of sexual selection male fitness may be increased by adopting a more dangerous strategy if this gives an overall increased insemination rate. Thus males of the same RHP as females may have a higher fitness budget for fighting over, say, food - because being in peak condition may affect male fitness more than female fitness because of intrasexual competition.

When asymmetries in RHP are used to settle conflicts conventionally, then why not cheat?, why not exaggerate or even fake one's signalling of high RHP?, why not always signal dominance?, why not fake the cues used to assess asymmetry?, why not conceal one's intentions to either flee or escalate? Prima vista, it would seem highly advantageous to give false information - and there is always the temptation to 'lie' - but there are severe costs attached to faking. For example, the more obvious the asymmetry the more costly (in terms of energy, time, and risk of injury) it will be to fake it. A falsely signalled commitment to escalate a fight may result in serious injury or even death if the cheat cannot live up to it. Some phenotypical properties (such as age, sex, small size, etc.), of course, cannot be faked at all, and these may be used as the most reliable cues and badges of status (Zahavi, 1977). Furthermore, in social species where individuals frequently encounter and individually recognize each other, cheats may be rather easily discovered.
In general, when costs are not prohibitive and cheating brings temporary advantages, one may expect an arms race, a run-away selection of cheating and
countervailing ability to detect cheaters (e.g., Andersson, 1980). But such circumstances are probably not very common. In most cases, the costs of cheating/faking/lying are substantial and therefore these deceptive behaviors are unlikely to evolve. At least in these contexts, honesty may be the best policy (e.g., van Rhijn \& Vodegel, 1980).

### 1.3.8 The Evolution of Territoriality

'Home range' is the area that an animal learns to know thoroughly and habitually patrols (Seton, 1909; Burt, 1943), and which must satisfy all of its bioenergetic needs (Gittleman \& Harvey, 1982), while the 'core area' is the area of heaviest regular use within the home range (Kaufmann, 1962; Jennrich \& Turner, 1969). The home range must be large enough to yield an adequate supply of energy. At the same time it should ideally be not much greater than this lower limit, because the animal will unnecessarily expose itself to predators by traversing excess terrain (E.O. Wilson, 1975).
Territory' is an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement (Noble, 1939; J.L. Brown, 1964, 1975; E.O. Wilson, 1971, 1975; Cf. DysonHudson \& Smith, 1978; Barash, 1982).
The territory need not be a fixed piece of geography. It can be 'floating' or 'spatiotemporal' in nature, meaning that the animal defends only the area it happens to be in at the moment, or during a certain time of day or season, or both (Cf. Leyhausen, 1965).
Territoriality, like other forms of contest competition, has taken protean shapes in different evolutionary lines to serve a variety of functions.
According to E.O. Wilson (1975) the exclusive use of terrain must be due to one of the following five phenomena: (1) overt defense, (2) repulsion by advertisement, (3) the selection of different kinds of living quarters by different life forms or genetic morphs, (4) the sufficiently diffuse scattering of individuals through random effects of dispersal, or (5) some combination of these effects. Where interaction among animals occurs, specifically in the first two listed conditions, we can say that the occupied area is a territory.
Territorial behavior is widespread in animals and serves to defend any of several kinds of resources (food supply, access to females, shelter, space for sexual display, nesting, etc.). The following classification of function, presented by E.O. Wilson, is an extension of one developed for birds by Mayr (1935), Nice (1941), Armstrong (1947), and Hinde (1956):

Type A: a large defended area within which sheltering, nesting, and most food gathering occur.
Type B: a large defended area within which all breeding activities occur but which is not the primary source of food.
Type C: a small defended area around the nest.
Type D: pairing and/or mating territories (leks).

Type E: roosting positions and shelters.

Why should animals bother to defend any part of their home range? MacArthur (1972) proved that pure contest competition for food is energetically less efficient than pure scramble competition. This is a paradox easily resolved. Territoriality is a very special form of contest competition, in which the animal need win only once or a relatively few times. Consequently, the resident expends far less energy than would be the case if it were forced into a confrontation with conspecifics each time it attempted to forage. Its energetic balance sheet is improved still more it if comes to recognize and to ignore neighboring territorial holders - the 'dear enemy' phenomenon (E.O. Wilson, 1975).

Clearly, then, a territory can be made energetically more efficient than a home range in which competition is of the pure contest or the pure scramble form. But if this is the case, why are not all species with fixed home ranges also strictly territorial? The answer lies in what J.L. Brown $(1964,1975)$ has called economic defendability. Natural selection theory predicts that an animal should protect only the amount of terrain for which the defense gains more energy than it expends. In other words, if an animal occupies a much larger territory than it can monitor in one quick survey, it may find itself trotting from one end of its domain to the next just to oust intruders, an energetically wasteful activity.
Furthermore, territorial defense is curtailed if it exposes animals too much to predation. There is also the phenomenon of aggressive neglect: defense of a territory results in less time devoted to courtship, fewer copulations, and neglected and less fit offspring.
If there is less than enough for all of some requisite for reproduction - food, cover, mates, or nest sites - some individuals will probably receive less than others of the resource in short supply. The 'haves' would then leave more offspring than the 'have nots', other things being equal. The rewards of aggression depend on the stakes. If there is little to be gained by aggression and much to be lost by it, territorial behavior will be selected against. If there is much to be gained or guaranteed by aggression and little to be lost by it, territorial behavior will be selected for. Under steady-state conditions of competition, a norm for intensity of territorial behavior will most likely be established, with extremes in both directions selected against (J.L. Brown, 1964, 1975).
In short, the territorial strategy evolved is the one that maximizes the increment of fitness due to extraction of energy from the defended area as compared with the loss of fitness due to the effort and perils of defense (E.O. Wilson, 1975; J.L. Brown, 1964, 1975; Crook, 1968, 1972; Schoener, 1971).

The economic defendability model of territoriality was subsequently elaborated by Dyson-Hudson \& Smith (1978). Economic defendability has several
components that interact to produce a cost-benefit ratio. The costs of territoriality include (1) the time, energy, and/or risk associated with defending an area; (2) the possible diversion of time and energy from other necessary activities; and (3) the possible negative consequences of relying on a spatially limited area for resources. The benefits of territoriality are simply those that result from exclusive access to critical resources; however, this benefit is relative to alternative (nonterritorial) modes of resource utilization.
For any case of territoriality, the ratio of benefits to costs should exceed 1.0 (and probably by a comfortable margin). It can also be argued that adaptive processes in the long run will tend to produce optimal results and, thus, that the benefit/cost ratio for a territorial system should have an average value greater than the nonterritorial alternative available for the individual or group. The cost/benefit ratio of a territorial strategy is highly dependent on the pattern of resource distribution. For a general model of economic defendability, as presented by Dyson-Hudson \& Smith, the important parameters of resource distribution are predictability and abundance. Predictability has both a spatial component (predictability of location) and a temporal one (predictability in time). Abundance or density of a resource can be measured in several ways: in terms of average density over a broad area (the average for the territory or home range), as an average value within a particular type or microhabitat (within-patch density), and in terms of the fluctuation in density over time (the range of variability).
Resources that are predictable in their spatiotemporal distribution have greater economic defendability than unpredictable resources. A habitat where critical resources are predictable will be most efficiently exploited by a territorial system (holding other resource distribution parameters constant).
Geometrical models of foraging indicate that it is more efficient for individuals to disperse to mutually exclusive foraging areas when food resources tend toward a uniform distribution and are predictable (Horn, 1968; C.C. Smith, 1968). Unpredictability of resources results in lowered benefits of territorial defense (in terms of resources controlled), and, below a certain threshold, territoriality will be uneconomical or even unviable (J.L. Brown, 1964).
With a sufficient degree of resource predictability, clumping of individuals (coloniality) is expected to occur. Under these situations, efficient resource utilization may depend on the pooling of information about the location of ephemeral resource concentrations.
In general, increased average density of critical resources makes a territorial system more economically defendable, simply by reducing the area that needs to be defended and thus reducing defense costs. However, density of resources within a patch combined with a high degree of unpredictability reduces the economic advantage of territoriality. That is, with sufficient within-patch density and patch unpredictability, localized and ephemeral superabundances result, where the temporary glut of resources is more than can be consumed and thus is best shared (either actively or passively) rather than defended.

Table 1.3.9: Relationship between resource distribution, territoriality, and foraging strategy (after Dyson-Hudson \& Smith, 1978)

| Resource <br> Distribution | Economic <br> Defendability | Resource <br> Utilization | Degree of <br> Nomadism |
| :--- | :--- | :--- | :--- |
| A. Unpredict. Dense | Low | Info-sharing | High |
| B. Unpredict. Scarce | Low | Dispersion | Very High |
| C. Predict. Dense | High | Territoriality | Low |
| D. Predict. Scarce | Fairly low | Home ranges | Low-medium |

### 1.3.9 Dominance Hierarchies and Cost/Benefit Calculus vs. Innate Inhibitions

Popp \& DeVore (1979) analyzed aggressive competition in the context of social dominance theory. Perhaps the single most important conclusion emerging from this study is that dominance hierarchies are expected to be timeand resource-specific.
As we have seen, it is adaptive for an individual to be able to predict the outcome of an aggressive encounter; such an ability permits him to reduce costs by avoiding conflicts that will be lost and to increase benefits by competing to the end in encounters that he can win.
In species that form long-term associations among a small set of individuals, one method of predicting the outcome of a competitive encounter is by the recollection of past encounters with a specific opponent. Past competitive experience with a known opponent under circumstances similar to the present competitive interaction can be useful in estimating the cost-benefit function for the opponent in aggressive competition.
The best strategy for a subordinate individual who knows from past experience that it cannot win an encounter is to avoid the competition. It is this principle that is responsible for the often observed decline in the frequency of aggressive behavior when the members of a social group have had sufficient time to form dominance hierarchies.
Popp \& DeVore emphasize that both dominant and subordinate individuals must be viewed as actors that have been selected to display behaviors appropriate to the natural social environment for the maximization of their reproductive success. Dominance hierarchies do not exist because they bring harmony and stability to the social group, but as the consequence of self-interested actions, in the evolutionary sense, by each group member.

If an individual in an aggressive interaction terminates its aggressive behavior at or shortly after the time that its opponent gestures submissively, it will gain access to the disputed resource and on the average gain a net benefit for the entire interaction. If the winner continues to act aggressively toward the already submissive opponent, however, the situation changes substantially. If we assume that the victor continues the aggression with the intent to kill or seriously injure his submissive opponent, a new set of cost-benefit functions rapidly develop.
Since no cost of competition could ordinarily exceed the costs of a fatal injury or, alternatively, since the benefit of saving one's life is considerably higher than the benefit that could be derived from a disputed resource, the individual whose submissive behavior has failed to terminate its opponent's aggression, will under most circumstances, fight desperately in an all-out self-defense. By contrast, the only benefit for the potential assassin would be the elimination of just one of many competitors.
In addition, under natural conditions the submissive animal often has the opportunity to escape, and this further reduces the mortality directly attributable to aggressive competition.
Note that the preceding argument is not at all equivalent to the frequent assertion that organisms possess an innate inhibition against killing conspecifics: whenever differences between two competitors in intrinsic competitive ability times the maximum adaptive expenditure for aggressive competition are sufficiently large, killers can be favored by natural selection. Although there is a number of noteworthy examples of strategies favored by natural selection that lead to the killing of conspecifics (e.g., infanticide, fratricide, siblicide, cannibalism), the cost-benefit functions do not often meet such criteria (avian siblicide may be a more common adaptive strategy, however: See Mock, Drummond \& Stinson, 1990).

### 1.3.10 The Evolution of War?

The proposition that war may have evolved during hominid/human evolution may seem odd - even absurd - for those readers who are accustomed to regard war as a social institution and cultural invention of relatively recent origin, i.e., concomitant with the emergence of states or state-like structures.
Yet, it may be worthwhile to explore the possibility that war has evolved along with the emergence and evolutionary trajectory of the genus Homo. Many behaviors, traditionally considered to be uniquely human and of cultural origin, now have been shown to have evolved components, that is, to have been naturally selected. There is little doubt, for instance, that human sexuality or aggression (the agonistic behavioral system) do have such evolved components. And given the importance of these behavioral systems for the survival and reproductive success of the individual organism, such a state of affairs is not particularly astonishing, though many people are still very reluctant to
acknowledge any 'animal heritage' in human behavior. Identifying evolved components in human behavior is often misconstrued as being an excuse or a subterfuge: "Our unalterable human nature being what it is...". It is equally often condemned as 'bad', not only 'bad science', but intrinsically morally bad because it runs counter to every soothing illusion man has created for himself. Other critics would grant the existence of evolved components at the individual level of behavior, but would assert that it is quite another step - in fact, illegitimate or irrelevant or impossible or simply impractical - to even consider war, genocide and massacres, as the most gory and extreme forms of human collective violence, to have some evolutionary background.
Throughout recorded history, however, war has been a rather normal and accepted way of conducting disputes and settling conflicts of interests between political groups and other, e.g., ethnic, territorial, 'racial', tribal and other collective units. It is a sobering thought that the ideal of peaceful coexistence has seldom been on the priority list of nation-states during the history of Western civilization, and even in this decade, with its unsuspected resurgence of bitter ethnic mass murders - it seems utopian more than ever. It would, however, be too facile to ascribe this deplorable state of affairs to some kind of 'innate aggressiveness', 'beast-in-man-below-the-thin-veneer-of-civilization' or 'universally warlike human nature', or some other quasi-explanatory concept that obscures rather than clarifies the human condition. To aficionados of these and similar easy solutions I have very little to say. Rather, as the proverbial dwarf standing on the shoulders of giants, I intend to explore the evolutionary impact, as unbiased and sincere as possible, on the genesis and vicissitudes of war during the humanization process, or, at least, on the peculiar human cognitive and emotional make-up which underlies this collective destructive enterprise.

In evolutionary perspective, the main problems I intend to address in this study are (a) to explain why war or its nonhuman equivalent (violent and more or less organized intergroup conflict) is confined in the animal kingdom to the hominids/humans, at least one species of chimpanzee (Pan troglodytes), and, though in much lesser and milder degree and less orchestrated, in some dolphins, social carnivores (such as hyenas), and a small number of primates, such as baboons and macaques; and (b) to simultaneously explain the conspicuous absence of the nonhuman equivalent of warfare in mammals generally, and primates in particular. This absence of violent intergroup competition in these animals is especially puzzling because they all have interindividual agonistic behavior ('aggression') in their behavioral repertoires. A correlative problem concerns (c) the explanation of why it is universally males who are the warriors in humans and chimpanzees (in contrast to the social carnivores and primates in which females are prominently present in intergroup conflict); in other words, why warfare is such conspicuously sexually-dimorphic behavior. These are all ultimate-level questions. For the
corollary proximate-level questions of why human males fight in wars at all, their proximate motives, I shall review the pertinent literature.

### 1.4 The Study of Primitive War: A Brief History


#### Abstract

As a total phenomenon its dominant tendencies always make war a remarkable trinity composed of primordial violence, hatred and enmity, which are to be regarded as a blind natural force; of the play of chance and probability, within which the creative spirit is free to roam; and of its element of subordination, as an instrument of policy, which makes it subject to reason alone... These three tendencies are like different codes of law, deep-rooted in their subject and yet variable in their relationship to one another. A theory that ignores any one of them or seeks to fix an arbitrary relationship between them would conflict with reality to such an extent that for this reason alone it would be totally useless.


Karl von Clausewitz, Vom Kriege (1832)
Sometimes a standpoint is only a point of departure. Whether one returns to it depends on what is discovered during the journey. But in order to convey the fascination of the journey of exploration, it might help to make clear what the original standpoint was in the first place. For that reason a number of concepts as used in this book have to be (briefly) dealt with.
The term 'primitive', as used throughout the book, may give rise to some misunderstandings. So it seems only appropriate to make myself perfectly clear on this subject. I do not use the term 'primitive' in any negative or derogatory sense, nor in the sense of non-complex - primitive societies may in fact be more complicated than modern ones - but rather in the original Latin meaning 'primitivus': "of or belonging to the first age, period or stage" (Hallpike, 1979), and as such has no derogatory implications whatsoever. I prefer this term to substitutes such as 'simple', 'egalitarian', 'unstratified', 'preliterate or non-literate', 'tribal', band-level', 'prestate or non-state', 'acephalous', 'preindustrial' or, as one may find in older literature, 'savage'. It is roughly equivalent to what in German is called Naturvölker in contrast to Kulturvölker. In order to avoid unnecessary repetition, I shall alternately use the terms 'Man', 'humans', 'mankind', humankind' and Homo (sapiens) sapiens as equivalents and referring to the human species as a whole. There is no sexism involved, with one notable exception: As primitive warfare is predominantly a male business, the term 'Man' in the context of war may sometimes refer mainly to the male members of the species.
What is meant by warfare will be dealt with in some detail in the next chapter. It may suffice to say here that it generally denotes armed fighting between tribal or subtribal (such as moieties, clans, phratries, etc.) sociopolitical units. In blood feuds the minimum conflict unit above the individual level is the kinship group or the family.

After these preliminaries, I now return to the main subject of this subchapter,
which is a brief overview of the history of the study of primitive peoples in general and primitive war in particular.

### 1.4.1 Classical Sources

We are probably accustomed to think of the study of primitive war and warfare as a 19th and 20th century activity. Actually, observations of the war customs and habits - in fact, the first ethnographical accounts - of what were then described as savage or barbarian peoples, can already be traced back to Classical times. Although Aristotle had decreed that any war against animals and barbarians would be a just war, this did not prevent some Greek historiographers to look sometimes farther than their ethnocentric and civilized noses, and give fairly accurate accounts of the war practices of the nomadic peoples surrounding them. For these early observers war belonged to the natural order of things, a 'natural mode of acquisition' as Aristotle called it, plainly justified by the law-of-the-jungle or the Might is Right arguments, so the question 'why war?' - the question of causes or motives - did not customarily occur to them. Thucydides is the odd man out. In a surprisingly modern-looking analysis, he identified the root cause of the Peloponnesian War as a preemptive attack based on fear in the context of a power struggle and arms race: "What made war inevitable was the growth of Athenian power and the fear this caused in Sparta... The Athenians made their Empire more and more strong... [until] finally the point was reached when Athenian strength attained a peak plain for all to see and the Athenians began to encroach upon Sparta's allies. It was at this point that Sparta felt the position to be no longer tolerable and decided by starting the present war to employ all her energies in attacking and if possible destroying the power of Athens" (Book x, Ch. 4). Only the nature of the power that posed a threat to the Spartans has changed over evolutionary and historical time.
Among the primitive war practices reported by the ancient observers were:

## - Head-taking and scalping

Herodotus (Histories, iv, 64-66), the first comparative anthropologist avant la lettre, reported the practice of head-taking and scalping among the Scyths (whom he admired and therefore was not slandering, as Turney-High [1949] correctly observed). The Scythian warrior not only drank the blood of the first man he slew in battle but decapitated everyone he could. These heads were tokens of his right to share in the booty when the king distributed it. After the victorious Scythian warrior had taken an enemy head he removed the scalp and carefully prepared it. He proudly used the scalp as a napkin, often sewing many of them together to form a cloak. Sometimes a Scyth would completely flay an enemy for the purpose, and quivers made of flayed enemy arms were highly esteemed. The crania of enemies particularly detested were made into drinking cups.

Diodorus Siculus claimed that the Gauls, too, were head-takers. The Nordic Edda and Heimskringla rarely speak of head-taking, but they do mention the trait.

- Coup-counting

Tacitus (Germania, 30) reported coup-counting among the Chatti, who were so military that he admiringly writes: "[O]ther Germans may be seen going to battle, but the Chatti go to war". Their youths did not shave or cut their hair until they had killed an enemy, so cowards and weaklings remained unkempt. The band of elite warriors owned no property and did no work, always knowing that they would be welcome to anybody's food, which they wasted without regard for their host's welfare. Such behavior was a clear parallel to that of a Plains Indian military association (Turney-High, 1949).

- War captives

The Scyths used war captives to milk their mares for them, and finding them valuable, blinded them to make them docile and immobile. Their chronicler, Herodotus (iv, 2), ascribes such blinding to "their not being tillers of the ground but a pastoral race". The Scyths also sacrificed a vast number of war prisoners to their war god (iv, 62).

- (Lack of) discipline

Tacitus ( $\mathrm{G}, 6$ ) reported disciplined cooperation among the Germans. He $(G, 7)$ revealed that the traditional sib organization of the Germans, disciplined, subordinated, and welded into working order by the higher political authority, was one of the sources of their strength. Tactical units were bound together by the emotional value set on blood ties. This gave them strong incentive to courageous action. On the other hand, Caesar (De Bello Gallico, iv, 1) says that the Suebi would tolerate no battle discipline or direction, but strove by exercise, proper feeding and fasting, going naked in winter, and bathing in streams to make each individual a physical giant. The Thracians, according to the ancient chroniclers, could easily have threatened Greece, but their intense localistic attitudes prevented them. Herodotus ( $\mathrm{v}, 3$ ) called them one of the most powerful people in the world, and voiced the opinion that they would have been invincible if they had been able to effect internal unity. They could never accomplish this, and "herein therefore consists their weakness".

- Surprise attack and tactics

Tacitus (G, 43) said that the Harii, a tribe of Lugii, were a strong, fierce, artful people. They liked to paint themselves and equipment black and attack on the darkest nights, striking "like an army of ghosts". They were
universally successful, partly because of their phantasmal appearance, for "in every battle after all the eye is conquered first". The same author shows that the Scots could also make able use of the night surprise attack (Tacitus, Agricola, 25-6). The Germans, trying to cross the Rhine, used a surprise stratagem against the Celtic Menapii, pretending to retire to their own land. They went 3 days away to effect this stratagem, but in a single night the German cavalry wheeled and attacked, catching the Menapii complacent and unprepared. The Menapii could only die (Caesar, iv, 4). Herodotus (iv, 46-47) speaks respectfully of the 'terrible and able' Scyths, praising their superiority in tactical mobility. As horsed nomads they were expert mounted archers. Similarly, Caesar ( $D B G$, iv, 2) praised the Suebi. In cavalry combats they often dismounted to fight afoot. Turney-High (1949), our best source on primitive tactics and strategy, comments that dismounting in a cavalry melee requires the highest kind of courage. The Chinese historian Ssu-ma Ch’ien (Sima Qian, ca. 100 BC) described Hsiung-nu (Xiongnu) nomadic tactics and strategy in terms almost identical with those applied by Herodotus to the Scyths. We have, furthermore, information on war tactics of the Bellovaci (Caesar, v, 56) and the Iapydes (Appian of Alexandria, Roman History, x, 18).

- Duel

Cassius Dio (Roman History, iii, 6,7) describes a championship duel in the struggle for supreme power between the Albans and the early Romans.

- Loot and spoil, and spoiling for a fight

Tacitus ( $\mathrm{G}, 14$ ) commented on the Germanic youths' dislike of peace, how they would seek service under foreign chiefs if their own tribe were cursed by a long period of quietude. The chiefs also preferred war, for from war came loot, and by loot one could maintain a large retinue, could make gifts of fine horses and weapons, could give banquets, and earn a name for generosity.
"The chiefs fight for victory, the followers for their chief. Many noble youths, if the land of their birth is stagnating in a long period of peace and inactivity, deliberately seek out other tribes which have some war in hand. For the Germans have no taste for peace; renown is more easily won among perils, and a large body of retainers cannot be kept together except by means of violence and war... A German is not so easily prevailed upon to plough the land and wait patiently for harvest as to challenge a foe and earn wounds for his reward. He thinks it tame and spiritless to accumulate slowly by the sweat of his brow what can be got quickly by the loss of a little blood". Also the verdict of Herodotus (v, 4) on the Thracians is unequivocal: "[T]he best man, in their opinion, is the idle man, and the sort least worthy of consideration is the agricultural labourer. The most reputable sources of income are war and plunder".

## - Honor and courage

The honor motive is not as apparent in the literature on Eurasia as it is elsewhere, but it does appear. Scythian behavior, for example, resembled a Crow coup-counting council. The governor of each district held an annual wine feast at which all Scythian men who had slain a foe during the year dipped into the chief's bowl. Those who had killed several could bring two cups and drink from both. Those who had killed no one had to sit aloof in disgrace. Tacitus ( $\mathrm{G}, 14$ ) reports of the early German peoples: "On the field of battle it is a disgrace to a chief to be surpassed in courage by his followers, and to the followers not to equal the courage of their chief. And to leave a battle alive after their chief has fallen means lifelong infamy and shame. To defend and protect him, and to let him get the credit for their own acts of heroism, are the most solemn obligations of their allegiance".
Firm belief in a hereafter made the Germans and the Celts contemptuous of death. Caesar (vi, 14) said that the Gallic Druids taught the metempsychosis of souls as their cardinal doctrine, so that, fear of death being removed, the warriors could be incited to great valor. The Valhalla myth of the Nordic peoples was also a well-known fear-inhibiting idea.

## - Divination

Tacitus' (A, 11) remarks about the Britons being superstitiously reckless at times and cowardly at others has a familiar ring. Caesar (i,50) was once surprised that Ariovistus did not strike hard at him to win a decisive victory, but upon questioning the prisoners, he discovered that the German matrons, whose duty it was to foretell victory by lot and divination, had declared the heavens unpropitious and warned the king not to fight before the new moon. Also Tacitus (G, 3) said that the Germans divined the outcome of battle by ordeal. Fear could be repressed by entering only those battles the favorable outcome of which was assured. The Germans would not tolerate so much as a disciplinary blow from their commanders but submitted to death if the war divinity demanded it. The priests also carried "certain fetishes... and emblems into battle to insure success" (Tacitus, G, 7). Justin relates that a coalition of Celts under a petty chief named Catumandus attacked the Greek colony of Marseilles in about 400 BC , but were frightened away by some magico-religious omen.

## - Destructiveness

The devastation brought about by these peoples, in spite of their primitive technology, should not be underestimated. The Celts apparently left nothing standing when they conquered a country. Avienus (Ora Maritima) stated that the ravaging Gael always left desolation where prosperity once dwelt. And Herodotus complained about the Scythians' insolence: They scoured the country and plundered everyone of whatever
they could.

- The role of women

According to sources available, Eurasian women played a very great part in war. Caesar (i,51) certainly reported no lack of spirit among the German women in the band of Ariovistus. The Germans arranged their wagons so as to make retreat impossible, setting their women on them so that they would beseech the advancing men with tears not to deliver them to Roman slavery. Similarly, Tacitus (G, 7,8) said that the Germans placed the women and children where they could behold their valor. Wives and mothers supplied the men with food and exhortation. He said the Germans wrested many a victory from apparent defeat because the women bared their breasts with pleas that they fall not into enemy thralldom. Women egging men on to war is also a common situation in the Norse legends (Biarkmol Him Foinu, Heimskringla). The Ramayana has several passages in which wives and mothers behaved very much like those reported by Caesar and Tacitus. The Aryan women, if we are to believe the hymns (e.g., Taittiriya Samhita) were, like the Nordic women, Valkyr fighters. The hymns also relate that the non-Aryan girls formed troops against the invaders which were in no way inferior to the male battalions (RigVeda, V, 51,80 et passim).

## - Peaceability

The classical literature does not only rhapsodize the warlike qualities of the 'barbarians', it also provides striking examples of peaceful peoples. In describing the Libyan tribes, Herodotus (iv, 174) mentions the Garamantes: "Further inland to the southward, in the part of Libya where wild beasts are found, live the Garamantes, who avoid all intercourse with men, possess no weapons of war, and do not know how to defend themselves". The name of the tribe is probably corrupt, and the actual existence of this people may be doubted, but Herodotus tells the story matter-of-factually, without apparent astonishment about how such a defenseless people could have survived in his rapacious and predatory world.
Similarly, he (iv, 26) relates of a certain Scythian tribe: "These people are supposed to be protected by a mysterious sort of sanctity; they carry no arms and nobody offers them violence; they settle disputes amongst their neighbors, and anybody who seeks asylum amongst them is left in peace. They are called Argippaei".
Tacitus (G, 46) states of the Fenni at the end of the then-known world (and probably the early Finns): "The Fenni are astonishingly savage and disgustingly poor. They have no proper weapons, no horses, no homes". And yet "Unafraid of anything that man or god can do to them, they have reached a state that few human beings can attain: for these men are so
well content that they do not even need to pray for anything".
Even among the bellicose early Germans there were exceptional tribes. Tacitus ( $G, 35$ ) admiringly says of the Chauci: "They are the noblest people of Germany, and one that prefers to maintain its greatness by righteous dealing. Untouched by greed or lawless ambition, they dwell in quiet seclusion, never provoking a war, never robbing or plundering their neighbors. It is conspicuous proof of their valour and strength that their superiority does not rest on aggression".
Also the Cherusci "have been left free from attack to enjoy a prolonged peace" (G, 36).
To conclude this section with a touch of the hilarious, Herodotus tells the tragicomic story of the Psylli in Libya: "The neighbors of the Nasamones are the Psylli - but they no longer exist. There is a story which I repeat as the Libyans tell it: that the south wind dried up the water in their storage tanks, so that they were left with none whatever, as their territory lies wholly within the Syrtis. Upon this they held a council, and having unanimously decided to declare war on the south wind, they marched out to the desert, where the wind blew and buried them in sand. The whole tribe was wiped out, and the Nasamones occupied their former domain".

I have dwelt somewhat on these classical sources, partly accumulated by Turney-High (1949), because here we already find virtually all the ingredients which characterize primitive war, as will be seen later: magical head-taking, scalping, victory-gloating, mutilation of the slain, coup-counting, the honor motive, the warrior cult, the sneak attack and ambush, magic and superstition; whereas other features, such as disciplined cooperation, almost transcend the boundaries of primitive war, almost go beyond the 'military horizon' as Turney-High (1949) would put it, because it is much more characteristic to find that each warrior is a soloist, performing on his own stage for his own glory. Discipline and coordination in battle provide the watershed between the warrior and the soldier.

### 1.4.2 The Widening of the Eurocentric World View

After the Classical period, the Dark Ages descended upon Europe, and the scene is replaced to the Arab world, where the vast continent of Africa gradually became to be explored (and exploited). Herodotus, of course, was the first to describe (from hearsay) the Egyptian and Libyan peoples, and there are other Classical sources on Africa (Strabo, Seneca, Pliny the Elder, Claudius Ptolemeus, Hanno, Kosmas Indikopleustes), but in general the more reliable information stems from Arab sources.
Northern Africa was to experience a long and dramatic sequence of colonization by Carthaginians, Greeks, Romans, Vandals, Byzantines and Arabs. The kingdom of Ghana was first mentioned in writing by an Arab
author of the 8th century, al-Fazari, while three centuries later the Moorish geographer al-Bakri of Cordoba described the people and their rituals, mentioning among others the institutions of divine kingship and human sacrifice. The kingdom of Kanem (near Lake Chad) was mentioned by al-Yaqubi (9th century), while the 10th century writer al-Muhallabi made it clear that it was a divine kingdom with absolute power. Al-Masudi, great explorer and geographer, referred to a divine kingship state in the hinterland of modern Mozambique ( $\pm 922$ A.D.). Ibn-Battuta (b. 1304) penetrated Africa as far as Timbuktu and Mali. There are also some Chinese sources on Eastern Africa: Tuan Cheng-shih (9th century), On Yang-Hsin (1060), and Chao Ju-kua (1226).
Ibn-Khaldun of Tunis (1332-1406), in his Introduction to History (1377), was the first to formulate the so-called Überlagerungs-theory of the origin of the state, which is essentially a conquest theory - victorious nomadic pastoralists settle permanently among the conquered sedentary horticultural or agricultural people as overlords - and he may be considered to be one of the founders of the so-called 'conflict school' of sociological thought.
So here we find the first theorizing on primitive war and its possible role in state-formation, a recurrent theme in the pertinent literature up till today, and reaching its zenith among the Social Darwinists (See Holsti, 1913).
Africa largely remained terra incognita until far into the 19th century. In the meantime, reports from explorers, ethnographers and missionaries about African tribal warfare had been accumulating to such an extent that the African Negro was considered to be the most warlike 'race' by Davie (1929), whose monograph on primitive war, still firmly rooted in the Social-Darwinist tradition, is the classic on the subject, although, unfortunately, rather one-sided. One cannot escape the impression, however, that much of this havoc (and tribal war in Africa could be devastating in its ferocity, lethality and sequelae) has been caused, directly or indirectly, by European colonialism and the New World demand for slaves.

### 1.4.3 The Age of the Philosophers

In Europe, meanwhile, the Scholastic thinkers had incorporated the classical sources, such as Aristotle, Plato, and the Stoa, in their body of knowledge on war, though they were preoccupied more with the justification of contemporary wars than with war causation in general.
By this time 3 basic paradigms on human nature in relation to war had emerged: (a) Dualism (Plato, Spinoza) which saw the fundamental cause of war rooted in the eternal conflict between rationality and passion; (b) the Augustinian perspective which saw the inevitability of war rooted in Original Sin and Divine Revenge; and (c) the Thomist paradigm, which envisaged man as an essentially rational and perfectible being, who was not doomed to wage wars forever by some metaphysical imperative.

The latter paradigm was to have a profound influence on the Encyclopedists and Philosophes of the French Enlightenment. Political philosophy of that time centered on matters of state (Raison d'Etat) in relation to war (Dante, Nicolas of Cusa, Bodin, Macchiavelli). Most influential was Thomas Hobbes' Leviathan (1651), in which Hobbes postulated the thesis that the status naturalis of mankind was a status hostilis resulting in a "bellum omnium contra omnes" (war of all against all). As the reasons for this state of affairs he identified competition as well as the universal human motives of diffidence, glory and power ("I put for a general inclination of all mankind, a perpetual and restless desire for power after power, that ceaseth only in death"). Existential fear would then lead to the Social Contract. Hobbes' views were contradicted by Montesquieu and, especially, Rousseau (Contrat Social, 1762): in the status naturalis, in the absence of property, war would be impossible. By their contemporaries these antithetical views were made the stake of the controversy whether original man, man in the state of nature, was peaceful or warlike. This so-called Hobbes-Rousseau controversy (treated more extensively in Ch. 2), has dominated the anthropological and sociological literature to the present day. Most philosophers (Spinoza, Locke, Kant) and the founders of international law (such as Grotius) did not envisage peace as the natural state of mankind.

The discovery, and subsequent ravishing and subjugation, of the New World by the Spanish Conquistadors in the wake of Columbus, Cortez, Pisarro, etc., led not only to the destruction of entire civilizations like the Inca and Aztec, and the extermination of numerous primitive societies, but also to anthropological and ethnological information on a totally unknown, novel kind of human being: the American Indian. A dazzling, kaleidoscopic variety of culture patterns and sociocultural levels were to intrigue the observers.
Columbus had brought back some Indians from the Caribbean region to present them to the Spanish court (One century later these Caribbeans were extinct). But the real introduction, from our point of view, to the people in their natural state and habitat, was a book by a German sailor, Hans Staden (1557), who had been washed ashore in South America after a shipwreck, and spent some time among the people we know as the Tupinamba (Brazil). The title of his book has some curiosity value: Wahrhaftige Historia und Beschreibung eyner Landschafft der wilden nacketen grimmigen Menschfresser Leuthen in der Newenwelt Amerika gelegen, etc.. Staden described the cannibalism and war customs of the Tupinamba in some detail (though doubt has arisen recently about its authenticity: cf. Arens, 1979). The book inspired Michel de Montaigne to write a thoughtful essay "On Cannibalism" (1580).
(To be sure, there are even older sources: e.g. the book Historia de los Indios de Nueva España by Motolinia already dates from 1541).
In the wake of the Conquistadors, who had come to plunder, and the first settlers, who had come to stay, followed the missionaries, who came to
convert. De las Casas had already appealed to the Conquistadors to save the souls of the Indians instead of killing them off. In practice, the Conquistadors had no pangs of conscience in saving the eternal souls and killing off the ephemeral bodies of the Indians.
In North America Jesuit missionaries and explorers like Charlevoix, Lafitau, Le Petit and LeJeune gathered a cornucopia of information on the daily life and war and peace customs of numerous North American Indian tribes or nations, as they were generally called. The accounts and letters left by the missionaries have been collected in The Jesuit Relations and Allied Documents, a multivolume publication edited by Thwaites (1897-1901), which still is a real Fundgrube for the student of primitive warfare.
These, and other, accounts had another important effect. They led to the first really empirical investigation of primitive war: An Essay on the History of Civil Society by Adam Ferguson (1767). His conclusion was unequivocal: "We had occasion to observe that in every rude state the great business is war; and that in barbarous times, mankind, being generally divided into smaller parties, are engaged in almost perpetual hostilities".

### 1.4.4 War as a Cultural Invention

Totally different conclusions were reached, however, by 19th century anthropologists, whose ethnological compilations and inventories began by now to appear with some regularity.
Lewis Morgan (Ancient Society, 1877), for instance, posited the original communism of primitive societies. This was gefundenes Fressen for Friedrich Engels, who based his Origin of the Family, Private Property and the State (1884) on Morgan's work. It was only when surplus production and socioeconomic classes appeared on the scene, he asserted, that class struggle and war did arise. In primitive societies, in which there is no surplus production, consequently there can be no war. This view of war as macroparasitism, as a predatory enterprise and cultural invention was to be the orthodox doctrine of Marxism-Leninism, as well the leitmotif of many non-Marxist historiographers (See Ch. 5).
The idea that war, the institution of war, is a cultural invention proved to be attractive to many cultural anthropologists. Man an sich would be peaceful, it is culture that transforms him into a belligerent being. The names of Margaret Mead, Ruth Benedict, Dewey, Malinowski and White come immediately to mind. And indeed, the idea has an optimistic ring about it. When war is 'only' an invention (Mead), it can also be 'dis-' or 'uninvented' and abolished: there is no arcane force or biological necessity which compels us to go on slaughtering one another in saecula saeculorum.
Yet, such a view carries its own problems. Very few, if any, of the cultural inventionists ventured to pose further questions: why was war 'invented' in the first place; why was it invented in so many cultures; and, crucial question, why
did supposedly peaceful human beings invent cultures in which war could be invented?
A peculiar offshoot of cultural inventionism was the short-lived school of diffusionism (e.g., Perry, 1917), which held that warfare was uniquely and exclusively invented in predynastic Egypt, and subsequently spread from this focal point over the entire globe by means of cultural diffusion. It proved not too difficult to point out the limitations and identify the fallacies involved in this approach (e.g., Q.Wright, 1942). Like old soldiers who never die but just fade away, the diffusionist theory was gradually abandoned rather than refuted.

### 1.4.5 The Rise of Academic Anthropology

I will use the term anthropology in the broadest sense to include both anthropology and ethnology, ethnography, ethnohistory, etc. in order to avoid unnecessary repetitions. Already in 1590 José de Acosta invented the term 'moral history' to designate what was later to be called ethnography, i.e., the description of customs, rites, ceremonies, laws, government and wars of Indian peoples. Even before him, in 1520, Johann Boem had published a general work comparing the customs of European, Asian and African peoples: Omnium gentium mores, leges et ritus ex multis clarissimis rerum scriptoribus... super collectos (Cf. Rowes, 1964; Godelier, 1977). Modern academic anthropology began to take shape before the middle of the 19th century. Around the fin-de-siècle it had become a well-established discipline. The early anthropological treatises on primitive war were, with a few exceptions, predominantly compilative, casuistic, and illustrative in character, rather than explanatory (in the sense of theory building and empirical testing of hypotheses derived from the theory), while sources were used selectively to demonstrate man's original belligerence or peacefulness, or whatever one was out to prove (e.g., Spencer, Jerusalem, Molinari, Holsti, Sumner, de Lapouge, Steinmetz, van der Bij, Waitz, Hellwald, Ratzel, Knabenhans, Weule, Vierkandt, Frobenius, Letourneau, among many others). The controversial opus magnum The Golden Bough by Frazer (1890), who had made an inventory of war ritual in primitive peoples, so impressed Freud that he devoted a chapter to it in his Totem und Tabu (1913). Freud tried to explain them as disculpation rituals (implying that also primitive man felt guilt and remorse about killing his fellow human beings) and he ventured to identify the psychodynamics underlying them. As may be inferred form the above, the Hobbes-Rousseau controversy was everything but dead when we enter the 20th century. It reached a new provisional climax in 1929, when the Dutch sociologist (who has entered history as the most fervent 'scientific' apologist of war) Steinmetz, and his, also Dutch, opponent van der Bij, both published their treatises on primitive war. Steinmetz (Soziologie des Krieges, 1929) reached the conclusion, which was in fact more a presupposition with data selected to match it, that man must have been aggressive, belligerent (and cruel) from the very beginning in order to have survived and evolved at all, while van der Bij (Ontstaan en eerste ontwikkeling van den oorlog, 1929), on the basis of a literature study of the most 'primitive' (he uses the term 'lowest') of all primitive peoples ever described, concluded: "The lowest peoples known to us do not, or very reluctantly and loathingly, resort to group fighting; offensive fighting does not occur at the lowest cultural level". Van der Bij submitted that 'primitive' peoples were non-belligerent because they were 'primitive'. Steinmetz retorted by stating that they were 'primitive' because they were non-belligerent: "Die Völker, welche nicht kämpfen und am wenigsten aggressiv sind, bleiben auf der niedrigsten Stufe stehen" [Those peoples that do not wage war and that are the least aggressive remain at the lowest cultural level]. It is curious to see that their respective bibliographies (which in the case of Steinmetz hardly deserves
the name) hardly show any overlap, which means that at that time there already was a substantial body of anthropological data on the subject, from which one could select one's sources to 'prove' one's own parti pris. The year 1929 produced, by the way, a bounty harvest for the study of primitive war: also Davie's The Evolution of War and Hoijer's The Causes of Primitive Warfare appeared in the same year.

### 1.4.5.1 Evolutionism

The concept of evolution as an ordering principle in cultural anthropology was proposed about 1840 even before Darwin's Origin of Species (1859). Evolutionism, the predominant school to the end of the 19th century, assumed a linear conception of human evolution and history: some groups progress more slowly, some faster as they advance from the simple to the complex, from the homogeneous to the heterogeneous, from the irrational to the rational (e.g. Spencer, Morgan, McLennan, Tylor). However, Morgan, and particularly Tylor, felt the necessity of introducing the concept of 'diffusion', or spread, of cultural traits because reality proved to be recalcitrant, thus suggesting that characteristics could develop independently and converge and that a people could leap over 'stages' of evolution by borrowing knowledge from others.
Lewis Morgan (Ancient Society, 1877), with Spencer and Tylor the founder of academic anthropology, demonstrated that the kind of social relations which dominate the organization of most primitive societies are kinship relations. He then showed how these kinship relations had an internal logic which had to be discovered through detailed studies of marriage rules and kinship terminologies. He assumed that these kinship systems had a historical sequence (mankind evolving from sexually promiscuous 'primitive hordes'), and that gradually the incest prohibition had been introduced, and marriage between blood relations in wider and wider categories had become tabooed. The human family' evolved from a primitive form of 'group marriage' to the monogamy of European nuclear families. Morgan also supposed that matrilineal kinship systems had preceded patrilineal ones. The differentiation of primitive peoples in their modes of life and linguistic stock was due to a "constant tendency to disintegration... followed by a complete segmentation" which characterizes tribal society. Tribal multiplication was accompanied by a state of permanent war among them since each tribe considered itself at war with all those with whom there was no formally signed peace treaty and even these were provisional. Constant segmentation and war was a powerful obstacle in the progress of 'savage' and 'barbarous' tribes. There were, however, some tribal societies who reached the 'civilized' stage, but at the price of the dissolution and disappearance of their clan and tribal organization.
Almost a century later, Sahlins (1961) and Service (1962) proposed a scheme of social evolution in four stages: the band, the tribe, the chiefdom and finally the state, whereby 'civilization' made its entry into history. Broadly speaking, this is also Morgan's, scheme with the concept of 'band' taking the place of the
'primitive horde' (Godelier, 1977). Cultural evolutionists did not, in general, envisage the possibility of devolution or involution which may found in the Werdegang of societies; they regarded it almost exclusively as a general, progressive, one-way movement. Steward (1955) and some others saw in cultural evolution a multilineal phenomenon. Godelier (1977) denies even that: "[T]here is no evolution in general', nor is there a 'general evolution' of mankind". Admittedly, this is a maverick position in social anthropology.

### 1.4.5.2 Social Darwinism

At the time when Social Darwinism (which might better be called Not-So-Social-Spencerism) flourished, roughly around the fin-de-siècle, the Apology of War, which had had a long tradition in European history, also reached its zenith. Some cross-fertilization is undeniable. In fact, Social Darwinism, with its zeitgeistiges emphasis on differential mortality ("Nature red in tooth and claw") as the principal agent of selection, added some biological arguments, such as 'improvement of the race', 'perfection of the species' to the gamut of arguments inherited from metaphysical and étatistic War Apology. A typical example of such a notion of differential mortality may be found in Quinton's Maximes sur la Guerre (1930): "La femelle propage l'espèce, le mâle, par sa mort, la sélectionne". It was a perfectly logical construction, given their premises, that if war is the agent of progress, the motor of human biological and cultural evolution, abolition of war was not only inadvisable but downright immoral. "Die wirkliche Aufhebung des Krieges wäre das erste Symptom des Todes" [The abolition of war would be the first symptom of death] as Steinmetz (1929) tersely put it. Darwin had already considered the role of primitive warfare as an agent of group selection in human evolution. This was theoretically elaborated by Bagehot (1872), Spencer (1873), and Steinmetz ( 1899 et seq.). Social Darwinism, as an amalgamation of evolutionism, selectionism, racialism, instinctivism, and functionalism, will be considered in more detail in Ch. 4.

### 1.4.6 The Major Contemporary Anthropological Schools

### 1.4.6.1 Ethnopsychology

Evolutionism, as a school of anthropological thought, had posited a universal human nature: all mankind was supposed to have a similar psychic outlook or mental equipment. This postulate was challenged by ethnopsychology (or cultural psychology), developing during the interbellum, based on the idea that culture conditions the very psychological makeup of individuals. In the 1930s Ruth Benedict found that the ways in which the Pueblo Indians thought and reasoned were strikingly different from the ways in which their immediate neighbors thought and reasoned, even though their geographical environment was virtually identical. Her conclusion was that each culture over the ages had evolved and given to its members a unique 'psychological set' or orientation toward reality and that this set actually determined how the members saw and processed information from the environment. Culture, in effect, affects the ways in which the mind works. Such 'cultural relativism', as it was to be called, led to many studies in culture and personality.

### 1.4.6.2 Marxism

In the second half of the 19th century another kind of evolutionism developed: that of Karl Marx and Friedrich Engels. Partly independent of anthropological evolutionism (Marx's Critique of Political Economy dates from 1859), partly linked to it (Engels' most important work appeared after Morgan's Ancient Society and made use of it), the Marxist theory laid stress on the causes of human societal evolution. A society was defined by its mode of production, on which its political, juridical, and ideological superstructures were allegedly based. These super-structures continued to exist after the mode of production had changed, and in the conflict that followed, this contradiction opened the way to a new type of society. Numerous anthropologists have taken the Marxist analysis into account, even if only to retain its historical view and materialist orientation, but to reject its economic determinism (Mercier, 1977). The contemporary American school of Materialism will be discussed in more detail in Ch. 4.
During the same period, especially toward the end of the 19th century, the tales of missionaries, traders, and travelling adventurers included an abundance of miscellaneous information that was collected in such works as Sir James Frazer's Golden Bough (1890) and Ernest Crawley's Mystic Rose (1902). These rather encyclopedic collections of customs, religious and magical practices, and other curious data were read with relish by the intellectual community; the theories that accompanied the collections were equally appreciated by evolutionary-minded anthropologists, as the theories were meant to establish an evolutionary sequence of magical, religious, and scientific phases in humanity's inexorable march of progress.

### 1.4.6.3 The Cultural History School

Frans Boas, a German-born American, was one of the first to scorn the evolutionist's search for selected facts to grace abstract evolutionary theories; and he inspired a number of students - Ruth Benedict, Alfred Kroeber, Margaret Mead, and Edward Sapir - to go out and seek evidence of man's behavior among men in their natural environments, to go into the field to gather facts and artifacts and record observable cultural processes.
He thus is known as the founder of the so-called culture history school of anthropology, which for much of the 20th century, dominated American cultural anthropology.

### 1.4.6.4 The 'Grand Diffusionists'

The large and influential American school of 'culture history' anthropologists led by Boas should not be confused with a distinct and smaller group of Austro-German diffusionists, led by Fritz Graebner and Wilhelm Schmidt, who constituted what has been called the 'culture-historical' school in Europe. These latter, too, had rejected classical 19th-century evolutionism, but they were nevertheless inclined toward painting grand theories - principally the theory that out of a few ancient cultural centers or civilizations, born quite separately, there had developed all the array of cultures existing today. Diffusion, or the spreading of culture traits, in their view, was the prime force of human development, and all cultural development could be traced to a few inventive centers. Because they termed these original centers "Kulturkreise" (or "cultural clusters"), they were also known as the Kulturkreise school of anthropology. The British diffusionists ( $\$ 1.4 .4$; see also Ch .6 ) were clearly inspired by this school.

### 1.4.6.5 The 'Sociological'School

In a similar way, Marcel Mauss in France influenced the characteristic tendencies of a whole generation of European sociologists and anthropologists, including Alfred Métraux and Claude Lévi-Strauss. He also influenced such men as the noted British anthropologists Bronislaw Malinowski and Arnold Radcliffe-Brown. In general, Mauss, like Boas, was insistent upon studying social phenomena as a system - but in a slightly different fashion. He conceived of systems as self-regulating or equilibrium-seeking, composed of elements that operate to maintain the integration or adaptation of the system. Mauss gave impetus, in fact, to what was called structuralism or the structural approach, which focussed more on society as an indivisible social organism than on society as an interrelation of individuals (the functionalist's emphasis).

### 1.4.6.6 Functionalism and Structuralism

Some schools of research that began to develop between the two world wars more or less vigorously rejected the historical approaches. According to the cultural functionalists, including the followers of Malinowski, the only way to explain facts was to define the function that they performed currently in a given culture. The aim of all anthropological research, they held, should be to perceive the totality of a culture and the organic connection of all its parts. Consequently, comparison did not make sense: each culture was a unique reality. History, moreover, made no more sense; a culture was to be interpreted at one point in time, as if the age and the origin of the elements composing it were immaterial. The only thing that counted was the function the elements performed now. Earlier anthropologists had envisaged 'survivals', customs or other cultural traits that survived from out of the past though no longer with any real function or meaning. But, according to the functionalists, everything current has some function. Whereas the name of Malinowski is associated with the school of functionalism, the names of Radcliffe-Brown and Lévi-Strauss are known as important proponents of present-day structuralism.
A structure is not a sum of social relations, which are only the primary material from which the observer extracts 'structural models'. A structure is a system of which the members of a society being studied are not aware or only partly so. The model that the anthropologist constructs from the system is valid when the model's operation can account for all the observed facts.
This exacting (and rather static) approach has has been applied to the study of kinship and marriage relations as well as myths (Mercier, 1977). In the study of primitive war, it appeared to be of minor significance.

### 1.4.6.7 The Correlationists

A next major step in the study of primitive war was the introduction of cross-cultural, macroquantitative research techniques, which, on the one hand, permitted crude statistical analysis and discovery of correlational patterns, and, on the other hand, necessitated the set-up of reliable (but rather static) data-bases and standard cross-cultural samples, for reasons of mutual comparison, such as the widely used Human Relations Area Files (HRAF) sample. Beginning with Hobhouse, Wheeler \& Ginsberg (1915) who subjected data on some 650 'simple peoples' to statistical analysis, (and on which Quincy Wright [1942] based his compilation), cross-cultural research permitted at least some concrete testing of hitherto speculative hypotheses and the sifting out of manifestly false ones. For example, the results of these earlier investigations were unequivocal: War, or rather belligerence, is a concomitant of increasing civilization (contrary to Steinmetz' "humanization-of-war" thesis). Later studies have, with some exceptions, tended to confirm this general diachronic pattern. One such exception, the study by Midlarsky \& Thomas (1975), whose investigation led them to conclude that "Whether a society is structurally complex and, therefore, differentiated, appears to have little bearing on its war experience", merits some comments. The term 'war experience' as these authors use it, lumps together and confounds two fundamentally different categories. If a people $A$ attacks a people $B$, they both experience war, but one is the attacker and the other the defender. The highly peaceful Hopi frequently had to defend themselves against raids of marauding surrounding tribes: they consequently had a great deal of war experience. But the crucial question is not how much war people experience, but why and when they wage offensive war. Obviously, not to make a distinction between offense and defense does not contribute much to better understanding of these vital (and lethal) phenomena. The relation between cultural complexity, societal development, and frequency and intensity of war, and other consistent correlates of primitive war will be considered in more detail in the next chapter.

### 1.4.6.8 Evolutionary Bio-anthropology

Since the 1950s, a kind of 'revival' took place in theory formation on primitive war, receiving its inputs from social and cultural anthropology with a strong functionalist and ecological-demographic orientation (White, Vayda, Naroll, Divale, Harris, Otterbein, Ferguson, and others), as well as from evolutionary biology, ethology and sociobiology (Lorenz, Eibl-Eibesfeldt, Tinbergen, E.O. Wilson, Alexander, Durham, and others), converging in their emphasis on 'realistic conflict'. Most sociobiologically-oriented theorists would, furthermore, subscribe to a number of theoretical premises, as Meyer (1987) has pointed out: (a) the adoption of a neo-Darwinian evolutionary framework which is mainly selectionist; (b) the consideration of genes as the unit of selection, which leads consequently to an intrinsically individualistic approach; (c) the consideration of kin selection; and (d) the acceptance of the inclusive fitness optimization or maximization principle as the central proposition of the evolutionary paradigm. Durham (1976) suggests a terse formulation of the underlying principle of 'phenotypic cost': "[T]here is a biologically limited amount of time and energy available to each organism... natural selection adjusts the genetic influences on behavior so that this time and energy... are spent in ways that tend to maximize the representation of a given individual's genes". These evolutionary bio-anthropological theories and their criticism constitute the subject-matter of Ch. 4 .

While these theories undoubtedly constitute the mainstream of present-day theorizing, one should not overlook the inputs from other disciplines, notably social psychology, psychoanalysis, sociology, political science, peace research (polemology), etc. These rather heterogeneous and kaleidoscopic contributions to our understanding of primitive war and its causation and genesis will be covered in Ch. 5.


[^0]:    ${ }^{1}$ It was also growing dissatisfaction with the rather static character of the Human Relations Area Files and its virtual monopoly position as a universal data base (though it is incomplete and unreliable: cf. Fedigan, 1986; Knauft, 1991), and the increasing number of discrepancies I seemed to discover between several other inventories and the sources I had uncovered, which prompted the Ethnological Inventory Project. Not hampered by any methodological constraints, I could freely indulge in the fascinating accounts of 'savages' reported by missionaries, travellers and adventurers from about the 16th century onward.

[^1]:    ${ }^{2}$ Van den Berghe (1991) has pointed out that "Properly understood, evolutionary theory is intellectually repugnant to most of us. It is not easy to accept that evolution is a meaningless tale told by an idiot". My attempt to explain the existence of a disgusting phenomenon (war) by means of a revolting theory (evolution) may not be particularly appealing to many readers.
    ${ }^{3}$ Strictly speaking, natural selection does not select directly for behaviors; it selects for the psychological processes that (in conjunction with the environment) underlie behavior (D. Brown, 1991). Evolutionary psychology attempts to discover the innate psychological processes that constitute (or are key ingredients in) human nature, that were shaped by evolution, and that may in our present environment - result in behavior that makes no sense at all in terms of maximizing reproductive success (e.g., Cosmides \& Tooby, 1987; Symons, 1989; Tooby \& Cosmides, 1989).

[^2]:    Behavioristic psychology assumed that the human mind was virtually a tabula rasa: it had little wiring, and that of a very general sort. But behaviorism, or extreme versions of it, has been shown to have severe limitations. Current thought - forcefully supported by data on the highly specific cognitive, emotional, or behavioral deficits that result from brain lesions in specific locations thus has it that the mind is wired in great detail. This restoration of the localizing or faculty theory of the brain, which had been swept aside by behaviorism, is further buttressed by lessons from the attempts to develop artificial intelligence and by evolutionary theory. Creating artificial intelligence has been much more complicated than was first thought, and constructing systems that duplicate the performance of even relatively simple mental tasks requires considerable preprogramming that is specific to the task and that is analogous to 'innate knowledge'. In other words, the model of the human mind as comprising general-purpose 'intelligence' finds no support in artificial intelligence. The relevant theoretical consideration is that in the course of its evolution the human species did not encounter general problems, it encountered specific problems, such as recognizing faces and detecting cheaters in social exchanges. We should no more expect a general-purpose mental organ to evolve than we should expect general-purpose anatomical or physiological organs (D. Brown, 1991; Cosmides \& Tooby, 1987; see also Fodor, 1983). These mental mechanisms, with very few possible exceptions, must be panhuman (universal) and must have evolved in the long period in which humans were hunter-gatherers.

[^3]:    ${ }^{4}$ For other reviews of, and positions and arguments in, this vast literature, see: Alexander, 1979, 1987; Bonner, 1955, 1980; Boulding, 1978; Boyd \& Richerson, 1980, 1981, 1983, 1985; B.Campbell, 1970, 1972, 1979; D.Campbell, 1972, 1975, 1983; Cavalli-Sforza \& Feldman, 1981; Crippen, 1992; Darlington, 1969, 1978; Dawkins, 1982; Dobzhansky, 1955, 1962; Dobzhansky \& Boesiger, 1983; Durham, 1976, 1979, 1987, 1990, 1991; Freud, 1930; Goldschmidt, 1966, 1969; Haas, 1990; Holloway, 1981; Kitcher, 1985; Kitihara-Frisch, 1980; Koestler, 1968; Lopreato, 1984; Lumsden \& Wilson, 1981, 1983; MacLean, 1987; Maxwell, 1984; Maynard Smith, 1975, 1982; 1989; McCauley, 1990; Mumford, 1961; Parker, 1985; Plotkin, 1982, 1988; Plotkin \& Olding-Smee, 1981; Reynolds, 1984; Richards, 1987; Richerson \& Boyd, 1978; Rindos, 1985, 1986; Ruyle, 1973; Sagan, 1977; Sahlins \& Service, 1960; Service, 1975; Stebbins, 1982; Tinbergen, 1968, 1981; Uyenoyama \& Feldman, 1980; Voorzanger, 1987; Washburn \& Howell, 1960; Washburn \& Moore, 1980; White, 1959; E.O. Wilson, 1975, 1978; de Winter, 1984. In Ch. 8 it will be argued that the concept of culture is not very helpful for an evolutionary reconstruction of the hominid trajectory.

[^4]:    ${ }^{5}$ The 'misfit' conception of man, as propagated by Lorenz, Tinbergen, Freud and many of their disciples, may be considered a revival of the doctrine of Original Sin - which has permeated Judeo-Christian culture ever since St. Augustine (354-430) - in biological terms. "Two of the most significant psychologists of the twentieth century", Barash \& Lipton (1985) commented, "Sigmund Freud and Konrad Lorenz, reinforced a pessimistic view of human nature by their inadvertent misapplication of Darwin's theory... Even worse, if it so happened that all other animals normally restrained themselves, and behaved 'for the good of the species', and selfishness and violence occurred only within Homo sapiens, then people really would be aberrant, biologically tainted with a kind of original sin. Konrad Lorenz and his generation of ethologists were apparently unaware of the ubiquity of animal violence, and thus they falsely attributed special malevolence to human beings".

[^5]:    ${ }^{6}$ Mathematically, an ESS is defined as follows: A strategy I is an ESS if the expected utility of I played against itself is greater than the utility of any other strategy J played against I. This can be written $E_{i}(I)>E_{i}(J)$, where $E$ gives the expected utility of the strategy in parentheses played against the strategy indicated by the subscript. In a population consisting entirely of individuals adopting strategy I, rare variants arising by mutation which adopted a different strategy J would not increase in frequency, and hence the population would be stable under mutation and selection. An ESS may be either a pure strategy or a mixed strategy if it consists of adopting one out of a set of pure strategies according to a set of preassigned probabilities. If so, a stable population could either be genetically polymorphic, with appropriate frequencies of individuals adopting different pure strategies, or it could be monomorphic, the behavior of all individuals being random in an appropriate way (Maynard Smith, 1978).

[^6]:    ${ }^{7}$ In more technical terms: The theory of kin selection is based upon the insight that an individual's fitness has two components: (1) fitness gained through the replication of its own genetic material through reproduction, and (2) inclusive fitness gained from the replication of copies of its own genes carried in others as a result of its own actions. When an actor behaves altruistically toward its kin, fitness benefits to kin also benefit the actor, but the actor's benefits are devalued by the coefficient of relatedness $(r)$ between actor and kin. The coefficient of relatedness represents the probability that two individuals will obtain copies of the same gene through common descent from a single ancestor. The precise genealogical relationship among kin determines the probability that both will share the same gene through common descent. In diploid species, identical twins share all genetic material $(r=1)$, while parents share exactly one-half of their genetic material with their offspring $(r=0.5)$, and share on average one-quarter of their genetic material with their grandchildren $(r=0.25)$. Hamilton (1964) was the first to show that altruistic acts toward kin increase the inclusive fitness of the actor only if the increment to the recipient's fitness (b) weighted by the coefficient of relatedness between them $(r)$ is greater than the decrement to the actor's fitness ( $c$ ), or $b \times r>c$. Hamilton's rule is sometimes expressed in an equivalent form as $K>1 / r$, where $K$ equals $b / c$. Under a specified set of conditions, altruistic behaviors are expected to conform to Hamilton's rule.
    For altruistic interactions to be favored by kin selection, the conditions of Hamilton's rule must be met. If an actor's behavior decreases his or her own fitness by two units $(c=2)$, but increases the fitness of a full sibling $(r=0.5)$ by five units $(b=5)$, then the ratio of $b / c(5 / 2=2.5)$ will exceed $1 / r(1 / 0.5=2)$. All other things being equal, a mother is expected to behave altruistically toward her offspring $(r=0.5)$ only if the benefits to her offspring are greater than twice the costs of her altruism $(b>2 c)$. The same female is expected to behave altruistically toward her first cousin ( $r=$ $0.125)$ only if the benefits to her cousin are greater than eight times her own costs $(b>8 c)$. Thus, altruism is expected to be selectively directed toward kin, and close kinship is expected to facilitate costly altruism (Silk, 1987).

[^7]:    ${ }^{8}$ On reciprocal altruism see also: Trivers, 1971, 1985; Alexander, 1979; D. Wilson, 1980; Dawkins, 1982; Van den Berghe, 1983; J. Moore, 1984; Seyfarth \& Cheney, 1984; Rothstein \& Pierotti, 1987; Cosmides \& Tooby, 1989.

[^8]:    ${ }^{9}$ On adaptivenes see also: G.C. Williams, 1966; Kummer, 1971; Lewontin, 1974; E.O. Wilson, 1975; Gould \& Lewontin, 1979; Wind, 1982; Trivers, 1985; Borgerhoff-Mulder, 1987; Betzig, 1989; Tooby \& Cosmides, 1990; and Crawford, 1991.

[^9]:    ${ }^{10}$ In more technical terms, the predictive power of sociobiology is limited by (1) The substrate being dynamic rather than static, because of the extremely complicated fabric of continuously changing gene frequencies and environmental interaction; (2) the large number of different genes involved as present in most survival machines; (3) the nonlinear relationships between gene frequencies and behavior characteristics; (4) the forces directing and determining gene selection being statistical (stochastic) in nature and implying time-inertia (Wind, 1982).

