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Introduction

Dennen, J.M.G. van der

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Introduction: On Conflict

Polemos pantoon pater (Heraclitus)

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, with their own dynamic and their own logic (e.g., Wilson, 1975; Barash, 1977; Alexander, 1979, 1987; Trivers, 1985; Huntingford & Turner, 1987; Low, 1993; Van der Dennen, 1995; Wrangham & Peterson, 1996). 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.

There is, as Pettman (1975) pointed out, no accepted or agreed list of the social units by which conflicts might be classified. To talk of conflict in intra-personal, inter-personal, familial, group, class, ethnic, religious, intra-state or inter-state terms is to assume, perhaps erroneously, that 'each kind of social unit, having its own range of size, structure, and institutions, will also have its own modes of interaction and thus its own patterns of conflict with other social units' (Fink, 1968) like and unlike itself. Such an assumption merits scrutiny on its own, since, despite the plausibility of some sort of analytical link between the parties to a conflict and the nature of the confrontation that ensues, the link should be demonstrated and not allowed to stand by assertion alone.

This volume is devoted to one type of analysis of conflict, the sociobiological one. In *The Sociobiology of Ethnocentrism*, a book closely related to many of the ideas and some authors of this volume, sociobiology was defined as 'the branch of biology that concerns itself with the explanation of social behaviour in all species, including our own. It is thus, essentially, evolutionary biology, and relies on Darwinian, Mendelian and Hamiltonian ideas – concepts such as natural selection, genetics, and, especially the individual's inclusive fitness – for its underlying explanatory schema' (Reynolds, Falger and Vine, 1987). Inclusive fitness theory, first proposed by Hamilton in 1964 and repeatedly referred to in this book, shows that genes will spread if their carriers act to increase not only their own fitness or reproductive success but also that of other individuals carrying copies of the same genes. A person's inclusive fitness is his or her personal fitness plus the increased fitness of relatives that he or she has in some way caused by his or her actions.

It may sound very deterministic or even 'geneticistic' to try to explain social phenomena on the basis of some supposed underlying biological process, but that would be too restricted an interpretation of the effort to draw attention to biology as one place to look. What is encouraging about a recourse to biology is that there is a body of theory and a wealth of empirical data relating to other species. This provides an excellent background against which to compare and contrast human processes and situations, the main focus of attention here. None of the authors in the present volume is proposing to reduce the study of conflict to biology, to account for it simply as any simple instinct. But all are alert to the existence of similar processes in animals and are trying to use the theory of inclusive fitness to explain the evolution of these processes.

However, a sociobiology of human behaviour would not be taken seriously if it explains in terms of fitness something that can be better explained in strictly cultural terms or in terms of the market. That is why sociobiology of any human behaviour can and must seek links with social psychology, social anthropology, sociology, economics, political science and even history.

Beyond that – and this is very important – it would be quite pretentious to assert that sociobiology could solve all questions that have arisen since the phenomena of conflict were studied in a systematic way. To know what these questions are and why it makes sense to add a biological-evolutionary oriented approach to the study of conflict and competition, it is worthwhile to draw some broad historical lines. Therefore, this introduction aims literally at introducing the reader to the traditional scientific discourse on conflict, which usually means *human* conflict. Then a condensed overview on the (socio)biology of conflict and competition tries to make the non-specialist familiar with the most relevant theoretical and conceptual problems in this field. Those readers, however, who want to cut short and demand an immediate answer on the question why a sociobiological perspective on conflict and competition is a valuable contribution, should skip the next three main parts of this introduction and turn straight to its fifth part.

The Study of Conflict in Perspective

Conflict may be defined as: incompatibility of interests, goals, values, needs, expectations, and/or social cosmologies (or ideologies). Ideological conflicts especially have a tendency to become malicious (cf. Berger & Luckman, 1966).

Webster's Dictionary definition: "Clash, competition or mutual interference of opposing or incompatible forces or qualities (as ideas, interest, wills)". Coser (1956) defined social conflict as "a struggle over values and claims to scarce status, power and resources in which the aims of the opponents are to neutralize, injure or eliminate their rivals".

McEnery (1985) suggests as a new definition of conflict: "the interaction of any two or more value systems". Conflict is either malignant or benign depending on whether the particular interaction of the value systems tends to destructive disruption or creative progress.

According to Galtung (1965), an action-system is said to be in conflict if the system has two or more incompatible goal states. In the case of one actor the conflict is called a dilemma, *l'embarras de choix*, or intra-individual conflict, consisting of incompatible motivational or behavioral tendencies (approach/approach, avoidance/avoidance, and approach/avoidance conflict: see Hinde, 1966 for a thorough review of this literature).

Distinction should be made between conflict, conflict attitude, and conflict behavior, which may be depicted as a triangle. A conflict process may get started in any corner of the triangle. One of the means of conflict resolution is to eliminate or incapacitate one or more of the actors in the conflict. This may be done either nondestructively or destructively. The latter we call violent conflict. "Thus we may distinguish between destructive and non-destructive conflict behavior, although this is, of course, a continuum and not a dichotomy. Two of the most celebrated propositions about conflict can now be made use of: conflict behavior tends to become destructive behavior (because of the frustration-aggression cycle) and destructive behavior tends to become self-reinforcing" (Galtung, 1965).

Conflict-resolution mechanisms: Chance mechanisms, oracles, ordeals, regulated warfare, fights, private duels, judicial duels, verbal duels, debates, mediation, arbitration, courts, voting (Galtung, 1965).

Fink (1968) defines social conflict as: “any social situation or process in which two or more social entities are linked by at least one form of antagonistic psychological relation or at least one form of antagonistic interaction. This emphasizes that while **antagonism** (which for the moment remains undefined) is the common element in all conflicts, there are a number of different kinds of psychological antagonisms (e.g. incompatible goals, mutually exclusive interests, emotional hostility, factual or value dissensus, traditional enmities, etc.) and a number of different kinds of antagonistic interaction (ranging from the most direct, violent, and unregulated struggle to the most subtle, indirect, and highly regulated forms of mutual interference), none of which is necessarily present in all instances of conflict. This is a disjunctive definition which subsumes any form of social antagonism, thus making the theory of conflict equivalent to a theory of antagonistic social relations in general”.

Taxonomy and dimensions of conflict: Objective vs. subjective; horizontal vs. asymmetrical; fractionating vs. cross-cutting; zero-sum vs. variable-sum; absolute vs. relative; realistic vs. projected; violent vs. nonviolent; perceived vs. nonperceived; regulated vs. unregulated; indirect (parallel striving) vs direct (mutual interference); unconscious vs. conscious; impersonal vs. personal; continuous vs. intermittent; communication absent vs. communication present; large admixture of cooperation vs. relatively pure antagonism; object-centered vs. opponent-centered; based on scarcity vs. based on incompatibility, inconsistency, etc.; economic goals vs. non-economic goals; nondisruptive vs. disruptive; etc.

Dimensions of conflict: number of actors, number of goals, level of complexity of actors (individual, group, state); etc.

Stagner (1967) distinguishes: size, duration, evaluation, intensity, polarization, regulation.

Two conflicting paradigms of conflict: cataclysmic vs. strategic (or Tolstoyian vs.

Clausewitzian) (Rapoport, 1966), and three models of conflict dynamics: Fights, games, and debates (Rapoport).

Two basic and polar types of conflict structures (Freeman, 1972):

(a) **Overlapping conflict** structures exist when opponent groups are cleaved apart by differences on all significant value fronts – economic, political, educational, religious, ethnic, racial. Adversaries are opponents on all. There are no cross-cutting attachments to common values. There is no common ground upon which to compromise, no incentive to negotiate. Opponents ascribe to each other less than human qualities reflecting their lack of shared values. Violence is condoned by both groups in order to protect against the extreme threat represented by the other.

(b) **Cross-cutting conflict** structures exist when opponent groups are in opposition over a limited number of cleavage fronts, but are allied in common cause in other significant conflicts. Actors in disagreement over one or more value preferences find shared attachments when they approach other issue areas. Here lay the roots of social cohesion. Cross-cutting cleavages over values stitch society together by facilitating constantly renewed willingness to negotiate disputes and seek ground for compromise. Total involvement of an actor in any one conflict against any single opponent is precluded. Roles and statuses include interaction with a range of opponents on some issues who are allies on other conflict fronts. Multiple involvement in cross-cutting social cleavages precludes polarization on any one axis and keeps social groups open to ideas and

innovations from each other. Cross-cutting cleavage patterns make for low propensities to engage in violence and for high propensities to tolerate change, deviance, and innovation.

Analyses on the societal level thus seem to show that differentiations and conflicts within a group can nevertheless maintain the overall cohesion of the group. This had already been hypothesized by Ross (1920) in his *Principles of Sociology*:

The chief oppositions which occur in society are between individuals, sexes, ages, races, nationalities, sections, classes, political parties and religious sects. Several such oppositions may be in full swing at the same time, but the more numerous they are, the less menacing is any one. Every species of conflict interferes with every other species in society at the same time, save only when their lines of cleavage coincide; in which case they reinforce one another...

A society, therefore, which is riven by a dozen oppositions along lines running in every direction, may actually be in less danger of being torn with violence or falling to pieces than one split along just one line. For each new cleavage contributes to narrow the cross clefts, so that one might say that society is sewn together by its inner conflicts. It is not such a paradox after all if one remembers that every species of collective strife tends to knit together with a sense of fellowship the contenders on either side (Ross, 1920: 164-5; quoted in Doise & Lorenzi-Cioldi (1989: 49-50).

It has often been pointed out (Bernard, 1951; de Vree, 1982; among others) that hostile stereotypes, prejudice, threat perception, general hostility, and aggression (however conceptualized) are more likely to be the result of conflict than its cause.

General Theories of Social Conflict

It must be recognized that general theories of social conflict (or at least conceptual frameworks, assumptions, and hypotheses oriented to the analysis of conflict in general) have been around for a long time, both in the social sciences and in the general culture. General orientations toward conflict are present in all cultures, and appear not only in social science but also in religious, ethical, political, and philosophical systems from Heraclitus to Hegel, Macchiavelli to Hobbes, and Locke to Mill (Sorokin, 1928, 1947, 1966; Singer, 1949a,b; Bernard, 1957).

Several writers trace the beginnings of the modern sociology of conflict back to Marx and to Social Darwinists like Bagehot, Gumplowicz, Ratzenhofer, and Oppenheimer (Sorokin, 1928; Bernard, 1950; Coser, 1956, 1967; Dahrendorf, 1959, 1967; Horowitz, 1962). As Angell (1965) has argued, these early sociological theories were not truly general since they did not deal with all forms of social conflict. Nevertheless, these theories (along with the theories of Pareto, Durkheim, Marshall, Weber, Freud, and many others) contain many concepts, assumptions, and hypotheses which greatly influenced later writers who did attempt to deal with conflict in general. By the late 19th century, highly general theories of conflict in physical, biological, and social systems were presented in such works as “Conflict in Nature and Life” (Patterson, 1883), “Les Lutttes Entre Sociétés Humaines et Leurs Phases Successives” (Novikow, 1896), and “L’Opposition Universelle” (Tarde, 1897). General theories of social conflict appeared in the works of Tarde (1899), Simmel (1903), Carver (1908, 1915) and others. Various mixes of these

and earlier theories, together with new contributions and applications of these theories to various kinds of social conflict, appeared in the general sociologies of such writers as Cooley (1918), Park & Burgess (1924), Ross (1920/1930), Von Wiese & Becker (1932), MacIver (1937), Lundberg (1939), and Sorokin (1947), and in general treatments of conflict by Lasswell (1931), Simpson (1937), Lewin (1948), Singer (1949), Wright (1942), Chase (1951), Lawner (1954), and Coser (1956), among others (Fink, 1968).

Again, various combinations of concepts, assumptions, and hypotheses from these earlier theories, together with game theory and other mathematical approaches, continue to dominate the general theories of conflict developed by such writers as Bernard (1951 *et seq.*), Mack & Snyder (1957), Boulding (1957, 1962), Dahrendorf (1958, 1961), Schelling (1958, 1960), Rapoport (1960, 1965, 1974), Galtung (1959 *et seq.*), Rex (1961), DeKadt (1965), Thurlings (1965), Beals & Siegel (1966), Coser (1967), and Stagner (1967).

(see also: McNeil, 1965; C. Smith, 1971; Kriesberg, 1973; Oberschall, 1973; Brickman, 1974; Duke, 1976; Eldridge, 1979; Himes, 1980; Schellenberg, 1982;)

Again, various combinations of concepts, assumptions, and hypotheses from these earlier theories, together with game theory and other mathematical approaches, continue to dominate the general theories of conflict developed by such writers as Bernard (1951 *et seq.*), Mack and Snyder (1957), Boulding (1957, 1962), Dahrendorf (1958, 1961), Schelling (1958, 1960), Rapoport (1960, 1965, 1974), Galtung (1959), Rex (1961), DeKadt (1965), Thurlings (1965), Beals and Siegel (1966), Coser (1967), and Stagner (1967). (For further commentaries, please see: McNeil, 1965; Smith, C. 1971; Kriesberg, 1973; Oberschall, 1973; Brickman, 1974; Collins, 1975; Duke, 1976; Eldridge, 1979; Himes, 1980; Schellenberg, 1982.)

A landmark in the history of the study of conflict has been the so-called Simmel-Coser propositions on conflict (Simmel, 1903; Coser, 1956). Some of their more counterintuitive findings include:

1. Conflict serves to establish and maintain the identity and boundary lines of societies and groups.
2. Conflict with other groups contributes to the establishment and reaffirmation of the identity of the group and maintains its boundaries against the surrounding social world.
3. Patterned enmities and reciprocal antagonisms conserve social divisions and systems of stratification.
4. A distinction has to be made between conflict and hostile or antagonistic attitudes. Social conflict always denotes social interaction, whereas attitudes or sentiments are predispositions to engage in action.
5. Conflict is not always dysfunctional for the relationship within which it occurs.
6. Social systems provide for specific institutions which serve to drain off hostile and aggressive sentiments. These safety-valve (*Ventilsitten*) institutions help to maintain the system by preventing otherwise probable conflict or by reducing its disruptive effects.

7. Aggressive or hostile 'impulses' do not suffice to account for social conflict. It has often been pointed out (Bernard, 1951; DeVree, 1982; among others) that hostile stereotypes, prejudice, threat perception, general hostility, and aggression (however conceptualized) are more likely to be the result of conflict than its cause.

8. Antagonism is usually involved as an element in intimate relationships. A conflict is more passionate and more radical when it arises out of close relationships.

9. Conflict with another group leads to the mobilization of the energies of group members and hence to increased cohesion of the group.

10. Groups engaged in continued struggle with the outside tend to be intolerant within. Rigidly organized struggle groups may actually search for enemies with the deliberate purpose or the unwitting result of maintaining unity and internal cohesion.

Dahrendorf (1958 *et seq.*) pictures contemporary sociology as split between two viable models of society. The consensus-and-equilibrium model is followed by many sociologists most of the time, but Dahrendorf prefers (as did Marx) a conflict-and-change model. He leaves the impression that there is no good way to bridge these two models. However, it can well be argued that the bridge has already been built by his fellow German sociologist, Max Weber. Weber's work provides a thorough analysis of diverse forms of social organization and how in them social norms come to be stabilized so that raw social conflict is rarely observed. But Weber's theory also is based upon assumptions about the fundamental role of power and conflict in society.

Duke (1976) is among those who recently have pointed out the bridge which Weber provides between conflict and consensus theories of society. In his able review of sociological theories of conflict, he shows a special appreciation for Weber both as a sociologist of conflict and as a sociologist of social order. The propositions Duke uses to paraphrase and summarize Weber's conflict theory can be used as well as a summary of the neo-Marxian position as developed by Dahrendorf:

1. Conflicts of interest are endemic in social life.

2. Power is differentially distributed among groups and individuals in any society.

3. Social order is achieved in any society through rules and commands issued by more powerful persons to less powerful persons and enforced through sanctions.

4. Both the social structure and the normative systems of a society are more extensively influenced by powerful persons than by weaker persons (true by definition), and come to represent the interests of these more powerful persons.

5. Social changes are often more disruptive to powerful persons than to less powerful persons. Powerful persons therefore generally favour the status quo and oppose changes that would reduce their power.

6. However, changes in a society occur as the result of actions by persons who stand to benefit from these changes and who accumulate power to bring them to pass.

Far from being always a negative factor or social pathology, social conflict may contribute in many ways to the maintenance and cohesion of groups and collectivities as well as to the cementing of interpersonal relations. Any relationship between individuals or groups necessarily involves conflictual as well as cooperative or integrative elements, however that relationship might start off (Coser, Gluckman, Blake and Mouton, North, Cooley, Deutsch, McEneaney etc.). The analogy of friction in physics illuminates the essential character of conflict as neither good nor evil. Friction impedes movement and has to be overcome if movement is to take place. But the initiation of movement is impossible without friction, which is therefore essential to movement.

Deutsch (1969) categorized conflict as to whether it is 'productive' or 'destructive'. This categorization was a major advance in removing the fog of misunderstanding of conflict as necessarily an undesirable force. However, the nomenclature rests on end results, 'production' or 'destruction'. It therefore does not fully reflect the fact that, because value systems are dynamic, any given conflict is not foreordained as to result. For these reasons, according to McEneaney (1985), it is more accurate to categorize conflict as either 'malignant' (i.e. tending to produce destructive disruption) or 'benign' (i.e. tending to produce creative progress).

The sociobiology of conflict, competition, and aggression

Barash (1977):

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. We can identify two basic ways in which individuals compete for such resources, **scramble** and **contest competition**.

Scrambles occur 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. If the resource is used up in the process, then the so-called winners of scramble competition are the individuals who have converted the largest part of that resource into copies of themselves, i.e., those that are most fit. Fitness in this case has been achieved by simply out-reproducing the competition, usually by being most efficient at garnering the resource in question. By definition, social interactions are excluded from this type of competition.

If, on the other hand, competing individuals interact directly with each other and use the outcome of such interactions to determine access to resources, then **contest competition** is

taking place. To the victor belongs the spoils, in contest competition. In scramble competition, the victor is simply the one that scrambles for the most spoils. This is an Easter egg hunt, in which every participant ignores every other and simply concentrates upon finding as many eggs as possible. In contrast, contest competition would be occurring if the participants first argued, fought, or somehow disputed among themselves, on the basis of which they decided who would look where, who would have first choice of the eggs collected, etc.

Aggression is 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. Just as animals ought to exert themselves to acquire important resources or enlarge their supply, thereby enhancing their fitness, they also ought to resist the loss of important resources, thereby avoiding decrements to their fitness. Accordingly, animals may respond to aggression by threatening back, fighting back, and, occasionally, signalling their submission and/or running away. All these encounter patterns are subsumed under the term **agonistic behavior**.

Archer (1988):

Competition is a term used by ecologists to describe the active demand by two or more individuals for a resource or requirement that is potentially limiting.

Nicholson (1954) distinguished between **contest** competition and **scramble** competition. Contest competition occurs when one individual obtains access to a supply of resources sufficient to maintain it, or enable it to reproduce, and it denies access to others. This form of competition includes not only aggressive behavior but also some indirect methods such as reproductive competition (see below).

Scramble competition involves each individual obtaining as much of the scarce resource as possible but without directly challenging the others. It occurs when the resource is widely distributed, and it differs from contest competition in that the less successful competitors are likely to obtain some of the resource.

A second (and independent) distinction is between **resource** competition and **sexual** competition (Wilson, 1975). Sexual competition involves access to receptive mates; it includes both contest and scramble forms. One form of sexual competition which is similar to scramble competition is unobtrusive mating, where a male sneaks up to one of a number of females which are being guarded by a 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.

The evolutionary rules underlying interspecific variations in competitive aggression for food resources have been well covered in a number of previous discussions, for example those of Brown (1964), Wilson (1975), Clutton-Brock & Harvey (1976) and Geist (1978). 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 aggressive competition. This will apply

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.

If it is advantageous for an animal to compete aggressively for food, it will be energetically more efficient for it to fight a relatively few times for an area which contains food than to compete for each item of food. Given such a broad generalization, we should expect all animals to seek to defend feeding territories either in groups, in pairs, or individually, unless it is not possible to defend their food supply in this way.

Huntingford & Turner (1987):

We can loosely divide the causes of such conflicts of interest between animals into two broad and overlapping categories, conflict over **resources** and conflict over other **outcomes**. Thus, conflicts of interest commonly arise when two or more individuals are competing for something which they both need but which is in short supply.

Conflicts over outcomes include: killing or survival of prey; occurrence of mating; occurrence of parental care; distribution of care between parents.

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. Where a conflict takes the form of competition for limited resources, the participants may effectively appropriate whatever is going by becoming increasingly efficient at locating and exploiting it; this is called **non-aggressive scramble-competition**.

Alternatively, competition may be sidestepped by **mutual avoidance**, either in space or in time. A more active response to a conflict of interest is to **meddle** with the activities of rivals. In some cases, a favorable outcome is gained by **manipulating** the behavior of other animals.

One potential response to a conflict of interest is to make active attempts to **physically coerce** other animals into giving up a disputed resource or into acquiescing to a particular outcome. Conversely, the victims of such attempts resist strenuously. In ecological terminology, 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 can be recognized by a collection of features: by the forceful (and deliberate) attempt to inflict harm (either physical damage or exposure to an aggressive display) on another (reluctant) individual; this may be accompanied by strong physiological and emotional arousal and often functions to space animals out or determine status. Perhaps it is best to think of aggression as a special case of manipulation in which the desired outcome is brought about by intense displays, which can if required lead to direct physical conflict and injury [cf. Barash's definition of aggression as the proximate mechanism of contest competition].

It is generally accepted that in both human and animal conflict the initiation of an attack (offense) is not the same as protection against such an attack (defense). 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 an abuse of language to include escape under the heading of aggression. Therefore this word is often replaced by the term **agonistic behavior** (Scott & Fredericson, 1951), which refers to a "system of behavior patterns having the common function of adaptation to situations involving physical conflict".

Game-theoretical (cost/benefit) analyses of animal conflict

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.

Furthermore there are costs involved in “aggressive neglect”.

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 worth fighting vigorously for a valuable resource.

The Hawk-Dove Game (Maynard Smith, 1974) and the concept of ESS

When animals compete with one another the behavior each adopts depends on what other individuals in the population do. The techniques of game theory, originally applied to human conflicts [notably Prisoners’ Dilemma], have been used to investigate which behavior is best for an individual to use in relation to what others are doing. Game theory treats evolution as a game in which the players use different patterns of behavior. These behaviors are termed **strategies** but conscious decision-making is not necessarily implied. Many games try to answer the question of how aggressive an animal should be when fighting over a disputed resource. For example, in the hawk-dove game a hawk always fights fiercely either until the opponent retreats or until one or other combatant is seriously injured. A dove, however, tries to settle the dispute amicably by displaying rather than fighting and will retreat if attacked. Hawks always beat doves but if they fight another hawk they stand an equal chance of winning or being injured. If two doves fight, each has an equal probability of winning; neither is injured but they both spend a lot of time displaying.

The best strategy to use depends on the resulting costs and benefits and the frequency of its use in a population. Thus if the benefits (of gaining the resource) exceed the costs (of injury), a hawk in a population of hawks will do better than a dove because the dove never reaps the benefits of winning. But if the costs are greater than the benefits, a dove in a population of hawks does better than a hawk because it never bears the costs of escalated fighting.

In the first case, where benefits exceed costs, the strategy of playing hawk is termed an **evolutionarily stable strategy (ESS)**. Such a strategy cannot be outcompeted by any other strategy defined in the model that might invade the population (dove in this case). Where costs exceed benefits, however, neither hawk nor dove is an ESS. The evolutionary stable strategy here is termed a mixed one: play hawk with probability p and dove with probability $p - 1$. At this evolutionary stable ratio the pay-offs in terms of costs and benefits of being a hawk or a dove are equal. (Note that an ESS is not necessarily the best or even an optimal strategy for the individuals involved).

Competition and Aggression

Theoretically, populations of two species may interact in 9 basic ways: (1) neutralism, in which neither population is affected by association with the other; (2) mutual inhibition competition type in which both populations actively inhibit each other; (3) competition resource use type in which each population adversely affects the other in the struggle for resources in short supply; (4) amensalism, in which one population is inhibited and the other not affected; (5) parasitism and (6) predation in which one population adversely affects the other by direct attack but is nevertheless dependent upon the other; (7) commensalism, in which one population is benefited but the other is not affected; (8) proto-cooperation, in which both populations benefit by the association but relations are not obligatory; and (9) mutualism, in which growth and survival of both populations is benefited and neither can survive under natural conditions without the other (Odum, 1971).

Competition of two species for the same resources is, in a way, 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 lead 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 species (intraspecific competition) or members of two or more species at the same trophic level (interspecific 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). It also matches the intuitive conception held by most modern ecologists concerning the underlying behavioral processes (Miller, 1967).

Aggression within animal species is almost always associated with competition. Insofar as aggressive behavior is adaptive, it can usually be regarded as a competitive technique and placed within our scheme as one of the devices of the “contest” form of competition. Since other forms of competition exist, aggressive behavior can be expected to be less common in nature than competitive behavior (Wilson, 1970; cf. Barash 1977: “Aggression is the proximate mechanism of contest competition”).

The following generalizations can be made about competition in animals as a whole:

1. The mechanisms of competition between individuals of the same species are qualitatively similar to those between individuals of different species.
2. There is nevertheless a difference in intensity. Where competition occurs at all, it is generally more intense within species than between species.
3. Several theoretical circumstances can be conceived under which competition is perpetually sidestepped (Hutchinson, 1948). Most involve the intervention of other density-dependent factors of the kind just outlined or fluctuations in the environment that regularly halt population growth prior to saturation.
4. Field studies, although still very fragmentary in nature, have tended to verify the theoretical prediction just mentioned. Competition has been found to be widespread but not universal in animal species. It is more common in vertebrates than in invertebrates, in predators than in herbivores and omnivores, and in species belonging to stable ecosystems than in those belonging to unstable ecosystems. It is often forestalled by the prior operation of other density-dependent controls, the most common of which are emigration, predation and parasitism.

5. Even where competition occurs, it is frequently suspended for long periods of time by the intervention of density-independent factors, especially unfavorable weather and the frequent availability of newly created empty habitats.

6. Whatever the competitive technique used – whether direct aggression, territoriality, nonaggressive “scrambling” or something else – the ultimate limiting resource is usually food. Although the documentation for this statement (Lack, 1966; Schoener, 1968) is still thin enough to be authoritatively disputed (Chitty, 1967), there still seems to be enough well established cases to justify its provisional acceptance as a statistical inference (Wilson, 1970).

Asymmetries in Animal Conflicts

Early game theory models assumed that the combatants in a fight were equal in all respects. Clearly this is not so and more recent models consider contests in which individuals differ. The most studied questions have been whether animals use these differences (asymmetries) to settle fights and to decide how much to escalate, and whether the way they fight conveys information about the asymmetries. The asymmetries between the combatants are of three possible types (Maynard Smith and Parker, 1976):

1. Resource-holding potential (RHP). One combatant may be better able to fight and defend a resource than the other. A large, obviously superior opponent might quickly win a dispute without any escalation to physical contact being necessary.

2. Resource value. One combatant may value a resource more highly than does its opponent. Food may be more valuable to a hungry animal than to a satiated one, for example.

3. A third type of asymmetry is not related to resource-holding potential or to a pay-off, being quite arbitrary. A convention such as ‘if the opponents are otherwise equally matched, the owner of a territory wins, the intruder retreats’ is of this type.

There is evidence of each type of asymmetry being used to settle a dispute. If the asymmetries are very weak or difficult to detect then the ownership convention alone may be used. Unnecessary and potential harmful escalation is thus avoided (Huntingford and Turner, 1987).

Assessment of Asymmetries, Intentions, and Badging

In asymmetric contests, it would seem advantageous to lie (i.e. give false information about for example RHP), but there can be costs to doing so; and the more obvious the asymmetry involved, the harder and more costly (in terms of energy and time or risk of injury) it is likely to be to fake it. Conversely, cues will be reliable only when they cannot be faked (Zahavi, 1977). Where assessment is by trial of strength, faking may be too costly: roaring contests in red deer stags, for example, are physically exhausting (Clutton-Brock and Albon, 1979).

We would expect evenly matched opponents to conceal their intentions (to attack or to retreat) during an agonistic encounter – there is no point in saying you are going to give up right at the

beginning of the fight because your opponent might also be prepared to give up later on. Whether or not an animal uses a display that might reveal its intentions about persisting or giving up the fight may be determined by the relative costs and benefits of that display. Displays can be time- or energy-consuming and an individual using them can face varying degrees of risk of retaliation so a combatant can afford to use high cost or high risk displays only if they are effective. Faking intentions may be possible within certain constraints (Maynard Smith, 1984), but the cost of lying may be high. A commitment to escalate may lead to serious injury if the cheat is physically unable to continue fighting and cheating will thus be limited.

Status signals or badges may be advantageous because they obviate the need for agonistic encounters. But if it is so advantageous, why do not all individuals signal dominance whatever their true status? There are several possible reasons why status signals can exist without cheats invading and taking over the population. In situations where individuals frequently encounter and recognize one another, cheats may be discovered. In addition, it may not pay some individuals to pretend to be dominant if (because of factors such as small size) they are not capable of living up to the demands of high status. Where encounters are most frequent between individuals of similar rank a cheat would often be involved in a contest with superior animals. Cheats may then be discovered or they may suffer costs as a result that outweigh the benefits of signalling dominance (Huntingford and Turner, 1987).

Dominance and Territoriality

Similar cost/benefit calculations have been applied to explain the variety of animal dominance hierarchies and territory holding. In general, animals appear to adjust their rank and territorial behaviour according to both costs and benefits.

Game-theoretical analyses of specific conflicts

Conflict between the sexes:

1. conflict over the number of mates;
2. mate guarding, sneak copulations, rape;
3. conflict over the quality of mates.

Conflict over parental care:

1. desertion and paternal confidence.

Parent-offspring conflict:

1. infanticide and cannibalism.

Sibling rivalry:

1. fratricide.

If a comparison were made, it is likely, according to Johnson (1972), that intraspecific killing occurs with about the same statistical frequency in man and other animals. Even more outspoken

is Wilson (1978), who states: ‘Although markedly predisposed to aggressiveness, we are far from being the most violent animal. Recent studies of hyenas, lions, and langur monkeys, to take three familiar species, have disclosed that individuals engage in lethal fighting, infanticide, and even cannibalism at a rate far above that found in human societies. When a count is made of the number of murders committed per thousand individuals per year, human beings are well down on the list of violently aggressive creatures, and I am confident that this would still be the case even if our episodic wars were to be averaged in.’

Why a Sociobiology of Conflict and Competition?

Why this book? Why a sociobiological perspective on conflict, after all those other works on conflict? We will point to various merits of this approach. There are several reasons why a volume devoted to sociobiology and conflict and competition is neither redundant nor superfluous – besides the obvious need to study conflict from *every* point of view, in the hope that we might better understand and come to terms with the problems of human conflict:

(1) There is considerably *more* competitive and conflictuous (not necessarily agonistic) interaction going on than was ever dreamt of, on all levels of organismic existence, from intragenomic competition, through intraindividual conflict, sperm competition, interindividual contest competition, to the many intricacies of coalitional aggression in primates and man. The idea that competition may exist even at the intragenomic level is a relatively novel one. It is explained thus by Wind (1984, p.13):

Assuming that natural selection ultimately takes place at the level of the genes (or even at that of the nucleotides) there must be another mechanism that hitherto has hardly been taken into account. So far, one has focused only on the competition between their survival machines, the individual phenotypes. However, there is likely to be also a more direct competition by what I have called *non-interphenotypic, intragenomic gene control* (Wind, n.d.), and what Dawkins (1982) called the ‘arms race’ between the genes. Such competition is suggested by combining the Selfish Gene Theory with molecular-biological data.

Wind suggests that three kinds of the latter are of interest here. In the first place there is gonosomal and autosomal gene exchange through meiosis and mobility of DNA elements. This implies not only interallelic but, in general, intercoding-sequence competition. Secondly there is replication and expression of genes depending on the action of others. For instance, suppressor and regulator genes have been shown to control the expression of others. Lastly there are genes causing segregation distortion (or meiotic drive), i.e. causing themselves to be present in more than half of the gametes (see Crow (1979); Dawkins, (1982); for the idea of sperm competition see Parker (1970) and Trivers (1985)).

(2) There is also considerably more *violent conflict* than was formerly assumed (for example, by the German ethological school), in the form of infanticide in a wide range of species (Hausfater and Hrdy, 1984), involving pup-killing and/or cannibalism; infant mortality resulting from mate- and nest-desertion; siblicide; disproportional mortality of omega-individuals being forced into suboptimal habitats; lethal and injurious fighting between males over females; rape and courtship

violence; predatory 'warfare' and slavery in the eusocial insects; to intergroup agonistic behaviour in primates, culminating in 'primitive warfare' in chimpanzees (Goodall, 1979 *et seq.*) and, of course, man. (For kin selection theory see Hamilton (1963 *et seq.*), Wilson (1975a) and Trivers (1985); for sex ratio manipulation and parent-offspring conflict see Trivers (1974, 1985).)

These new data provide a falsification (or at least partial refutation) of ethological assumptions on inhibitory blocks against the killing of conspecifics. Thereby it has become clear that drive concepts of aggression, with their emphasis on the idea of action-specific energies (Lorenz, Eibl-Eibesfeldt), have become either entirely obsolete, or may only apply to a limited class of agonistic acts. Sociobiology can show that there are evolutionary 'optima' for behaviours such as aggression.

(3) *Game-theoretical models* of the evolution of agonistic behaviour are increasingly becoming more veridical and more robust in their predictive/postdictive power, thus more and more unravelling and revealing the 'cold calculus of evolution' in which reproductive success is the only currency.

These models not only include analyses of actual fighting behaviour, but also the evolutionary rationales behind the 'battle of the sexes', parent-offspring conflict, and sibling conflict (for example, Trivers, 1985; Stamps and Metcalf, 1980).

(4) Renewed interest is also shown by human sociobiologists in the evolutionary bases and vicissitudes of hominid and human primitive war, its causes, motives, dynamics etc. In this context it may be observed that many sociobiologists have been very reluctant to make propositions on the human species, while others have not hesitated to make sweeping statements (for example, on the alleged universality of human warlikeness). Several chapters in this volume testify to the renewed and critical interest in primitive war. Some sociobiologists – just like Freud, Lorenz, and others before them – try to explain war by recourse to the aggressive dispositions of people. This is a notion being criticized in this book. A merit of sociobiology is, however, to focus attention on the question of how war and human nature go together.

(5) On the other hand, it is not only becoming increasingly clear where and when conflict and (agonistic) competition are to be expected, but also, and perhaps more importantly, where and when not. For example, when limiting resources (of whatever kind) are abundant, an organism should not engage in agonistic contest competition (aggression) because the same benefits can be obtained without it. Similarly, when resources are scarce, it will often be energetically more efficient to engage in scramble competition (foraging) than aggressive competition (Archer, 1988). (For a review of optimal foraging theory see Barash (1982).)

(6) A more thorough analysis of altruistic behaviour, and the evolution of cooperative behaviour (Voorzanger, 1988; Axelrod and Hamilton, 1981; Axelrod, 1984) has revealed many intricacies and may constitute the necessary counterpoise to an overemphasis of conflict and competition in sociobiological thought. (For cultural evolution theories of human cooperation see Campbell (1975) and Boyd and Richerson (1985).)

There are two main reasons why sociobiology should not be expected to provide easy answers to the intricacies of human social behaviour. One reason is inherent in the discipline:

While the basic paradigm of the sociobiology the selfish-gene concept is quite simple as well as scientifically quite valid, the difficulties in its application in behavioural analyses seem to increase exponentially when passing from viroids to 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 (Wind, 1984, p.18).

The other reason is more intricate and substantial. It has become increasingly clear that *Homo sapiens 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 (some 40,000 years or some 2000 generations ago) is – in evolutionary perspective – quite short. Therefore, many of our genes frequencies and behaviours are still oscillating without having reached yet a less disequilibrated state as is usually found among other species. Stated in more traditional biological terms, adaptation still has to occur, or, in even less technical terms, we are still in the wake of our evolutionary origin. After all, man's genetic make-up was shaped when he or she was living in small family groups. Thus, at that time the overlap of group, kin, individual and gene selection was probably greater than nowadays. Yet, our behaviour (including altruism) is determined by largely the same genes interacting, however, with a totally different environment.

Enigmatically, man often seems to show sociobiologically odd properties such as celibacy and other nonreproductive behaviours. Some of these properties may, in fact, very well have, at the individual level, a negative selective value, and may be in the process of being selected against.

Because of the above reasons *Homo sapiens sapiens* is likely to show behaviours that can sociobiologically be qualified as an Evolutionarily Quite Uncommon, Unstable Strategy (EQUUS), instead of an Evolutionarily Stable Strategy (ESS) (Wind, 1984). In our view, however, this does *not* imply that it is superfluous or irrelevant to combine new biological theories and methodology with the study of human behaviour. We very well realize that sociobiology does not give definite answers to many fundamental questions. But since when is that enough reason not to try to expand the limits of understanding, in the last instance of ourselves?

That is why the interested reader is invited to study carefully the chapters that follow. The book is organized in four parts, but each chapter can also be read on its own. In Part I three chapters present theoretical and empirical studies on conflict from a biological perspective. The first chapter provides an introduction to the extensive ethological studies of conflict and reconciliation in primate groups. The human dimension is focused on in Part II where social scientists and biologists discuss the relevance of sociobiology for the explanation of the timeless and cross-cultural phenomenon of enmity. Part III highlights a supposed important origin of modern man: so-called 'primitive' warfare. Discussion of the existing literature, development of new hypotheses in this field and a detailed empirical case study make this part the most voluminous one of the book. The shortest is Part IV, containing one chapter on the conflict *about* sociobiology. Because we think, however, that the general debate about sociobiology is very

important to everyone who is interested in – or disgusted with – sociobiology, we thought it appropriate to address the topic of controversy around it unambiguously in this volume.

Any study of conflict behaviour is also an exercise in human introspection. Animal conflict studies more often than not refer to problems which also exist in the human species. An evolutionary approach of conflict behaviour in general implies a preparedness to accept reductionistic argumentation to a certain degree. It also requires a relativization of the nature-nurture dichotomy, in particular relevant in the study of human conflict behaviour. Unfortunately, every effort to explain human behaviour with the help of (socio)biological axioms is risking to be categorized as an ideological justification of the social and political status quo. Political attitudes, such as a tendency to accept social inequality, racism and sexism, are seen by some as logically following from the premise that human behaviour and human biological evolution cannot be treated as completely separated compartments.

The political accusation that sociobiology is inevitably leading to conservative and even reactionary social views of the world, or supporting these, must be taken seriously, however incorrect the accusation may be. Of course, sociobiology can be abused to support political value judgements. Sociobiology, used in a very particular way, could provide the existing inequality between the sexes or Apartheid with a legitimation which *looks* scientific, especially for those who are not familiar with the generally accepted rules of the game called science. Nobody will deny that individual people, using sociobiology argumentation, sometimes have aired opinions which fall in the category of political abuse – although hard data on this abuse are quite scarce.

Is this situation really different from other disciplines, like genetics, archaeology, psychology, history or economics? Principally no, practically we think yes: it has happened far less than might be expected (and has been predicted by many radical anti-sociobiologists). Admitting that sociobiology can be abused politically is something very different from stating that inclusive-fitness theory, the essence of sociobiology, is a pseudo-scientific, reactionary political cover-up (Sociobiology Study Group, 1978; Rose (ed.), 1982a,b; Rose, Lewontin and Kamin, 1984; Levins and Lewontin, 1985. See for reactions against these charges Masters, 1982 and Falger, 1984). Personal values and motives do play a role in the research programmes of individual scientists, proponents and opponents of sociobiology. Ullica Segerstråle's contribution to this volume represents an interesting analysis of two well known Harvard based opponents. The question, however, is ultimately whether a contribution is made to the understanding of, in this case, human behaviour. Of course, we should not judge the results ourselves, but all contributors expressly want their work to be seen as an effort to create that understanding.

As far as reductionism is used here, it is not because individual human behaviour is considered only as a personal expression of the 'laws of human nature'. Nor does the use of inclusive-fitness theory in this volume imply teleology or genetic determinism. And finally, the cost-benefit calculus, which sociobiology shares with the hard core of economic theory, game theory and public choice theory, offers a model of explanation and prediction, not an accurate description of actual historical phenomena. So, whoever feels justified to draw political conclusions from any of the essays in this book, does so purposively contrary to the intentions of the authors and editors. The only extra-scientific commitment we have is the hope that the study of conflict from

an evolutionary perspective adds to the understanding of a vital category of behaviour in animals and man.

This is the introductory chapter by the editors in J.M.G. van der Dennen & V.S.E. Falger (Eds.) *The Sociobiology of Conflict*. London: Chapman & Hall, 1990, pp. 1- 19.