Chapter 6

DETERMINANTS OF CONFLICT OUTCOMES

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ABSTRACT

Analysis of individual differences in competitive abilities is an essential part of the interpretation of unequal access to resources. Here we develop and apply a model applicable when dyadic contest outcomes determine access to resources, including mates. Individual differences in fighting ability may be decisive in determining contest outcomes. The components of fighting ability (FA) include inheritance (FAi), condition (FAc), experience (FAe) and development (FAd) to and throughout senescence (FAs). Present fighting ability (FAp) is a dynamic entity that varies as the value of these components change, waxing and waning as costs are incurred in contests. Fighting ability contributes to the probability that opponents will enter into and persist with patterns of conflict behavior and prevail as contest winners.

Simulations identify the probabilities of gaining access to status and resources when FA determines contest winners following dyadic contests. A sequence of interactions between opponents produce frequency distributions of fighting ability within populations which contain and may provide information to contestants about their fighting ability compared with that of other population

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members. Individual win:loss records may be incorporated into individual experience, resulting in effective behavioral responses to the probabilities of winning subsequent encounters. The probabilities of improving rank by transferring from one to another linear dominance hierarchy are determined given the assumption that FA determines rank. We identify the relationship of fighting ability to contests for resources in a competitive arena where some individuals are excluded from resources. These simulations emphasize the value of diachronic observations of individual contest histories and outcomes.

When fighting ability is not decisive in determining contest outcomes and the distribution of resources, the relative effect of other parameters in doing so is enhanced. The analysis of competitive behavior promotes identification of separable parameters which sometimes have opposing effects. Determinants of these additional processes occurring during animal conflict are identified and their utility in separating behavioral relationships is considered. These determinants include social support (S) from additional parties in contests and resource value (V), a collection of several relevant parameters influencing motivation. Motivation (M), the propensity of individuals to enter into and persist with contests, is a diversely used term. But the processes and phenomena it incorporates cannot be discarded, because without its role in the analysis of individual differences, fitness consequences of behavior are necessarily analyzed exclusively as a function of V.

Studies of the relationship of the determinants of conflict outcome identified here have been and can be incorporated into general models of contest behavior. To determine their respective effect upon conflict behavior and contest outcomes, some components of fighting ability can be set equal by experimentation or ordering of field observations. We extend our model to groups of individuals arranged in linear dominance hierarchies and to the ideal despotic distribution where access to resources is contested by many individuals. We make predictions about the exact probabilities of winning under alternative circumstances. We suggest how animals might adjust their behavior if they were to use the estimates of personal fighting ability identified by simulations to estimate their probability of winning.

INTRODUCTION

Conflict behavior allows individual animals to maximize their probability of gaining access to resources including mates and to minimize their lifetime costs of doing so. There are several essential pieces of information a contender requires to accurately estimate its probability of winning a contest. These include assessment of personal ability compared with that of the opponent and assessment of the motivation of an opponent to contest access to the resource. While perfect information is seldom available, even imperfect information can provide an estimate of relative ability and motivation. Contests usually begin with communication in the form of visual, vocal or other displays. In some instances these signals may convey sufficient information to resolve conflict. Conventional conflict settlement in this sense may be derived from contestants' earlier experiences, and decisions in response to relevant communicated information may be based on a history of contests. However, in the absence of perfect information, estimates are and can only be probabilistic and opponents may decide to engage in physical contests to determine which will get access to resources. Several context and intrinsic variables may be involved in determining conflict behavior and contest outcomes, and these will vary among species, populations and even by context for an individual. Nevertheless there are fundamental common properties of contest behavior which, when identified, facilitate interpretation of the determinants of conflict behavior. We assume that fighting is energetically costly, and that animals would not opt to fight if resources were unlimited. They place a premium on communication and accurate assessment. We examine the set of general determinants of conflict behavior and identify possible mechanisms of assessment, decision making and fighting. We review past analyses of animal conflict behavior and expand on them to identify a complete set of variables required to specifically address the questions: When do animals fight for access to limited resources? What determines the outcome of a contest? The aim of this paper is: (1) to facilitate an empirical multivariate approach to understanding the mechanisms of conflict behavior by providing a theoretical construct, an idealized model, of the relationships between conflict variables and behavior and (2) to identify an informational context based on estimates of probability of winning contests within which individual animals are expected to operate.

The application of game theory to interpretations of animal conflict behavior provides a framework for understanding alternative contest strategies from an evolutionary perspective, and especially why, for example, some contests are settled without fighting. The game theory approach addresses contests at the level of the genetic population using simplified frequency-dependent alternative strategy sets (e.g., hawk vs. dove). Following the first applications of game theory to animal conflict behavior (Maynard Smith and Price 1973; Parker 1974), the game theory approach, with the concept of an evolutionarily stable strategy (ESS; Maynard Smith 1982a) as the linchpin of theoretical validation, became the dominating paradigm for empirical analyses of animal conflict. Although game theory has provided important insights into ultimate explanations of alternative strategies, this paradigm imposes constraints that inhibit further detailed analyses of the mechanisms involved in conflict at levels at which detailed empirical research is currently conducted. Current emphasis upon this single theoretical paradigm in animal conflict behavior merits critical review.

It was not the intention of early ESS models to identify mechanisms of animal conflict or to reveal specific determinants of contest outcomes. Nevertheless, behavioral observations of dyadic contests have been analyzed with game theory as the conceptual framework. Among the recent few quantitative empirical tests of ESS model predictions are cases which have explicitly failed to demonstrate a quantitative fit of observations to predictions (e.g., Brockmann et al. 1979; Hammerstein and Riechert 1988). When results do not match predictions from the models, the terms of the models may be adjusted (Brockmann et al. 1979; Parker and Rubenstein 1981) or additional terminology added to exclude a range of otherwise inexplicable results (e.g., paradoxical ESSs which have no biological explanation, but are said to account for a part of the observations, Hammerstein and Riechert 1988). When no explanation supports theory, results may be attributed to a lag in the adaptive process, with the conclusion that an ESS has not yet been reached (Riechert 1979) or cannot be attained by the subject population due to gene flow constraints (Hammerstein and Riechert 1988). Thus, inferences from observations failing to match predictions from models remain ambiguous, a problem identified by others for optimization approaches in general (e.g., Gould and Lewontin 1979). We suspect abandoning the constraint of evolutionary stability as a criterion for validity in empirical investigations of conflict behavior would facilitate analysis of the mechanisms of contest behavior within a more temporally proximate, complex and dynamic multivariate context.

Application of game theory to animal conflict behavior, because it is limited to population level analyses using a limited set of generalized variables, (e.g., resource holding potential (RHP) and resource value (V)) and a small number of alternatives within a strategy set, is insufficient to enable more detailed understanding of animal conflict behavior at the level of the individual, where empirical studies often focus. The condensed terms of game theory models are often insufficient to describe the several processes modifying contest behavior and determining contest outcomes, and it has become common practice to model conflict with the terms RHP, V and costs and then to discuss the findings in terms of additional parameters that might reconcile observations with a model. The problem with this approach is that there is no set of observations that cannot be fully interpreted. There is thus no possibility that a null hypothesis will be rejected. Furthermore, while determining whether or not a particular set of strategies is an ESS is an interesting question, it is beyond the scope and focus of most empirical studies (e.g., Olsson 1994). To investigate and understand the mechanisms underlying acquisition and control of contested resources from the perspective of the participants in a complex multivariate system requires a more complex set of determinants than those offered in game theory models. Here we review the variables of conflict behavior, including the generalized terms used in game theory models of conflict, to identify sources of confusion. Then we develop what we consider to be a minimum set of determinants required to analyze empirically the multivariate nature of animal conflict behavior.

We first focus on the intrinsic variable fighting ability (FA) and identify the set of determinants represented by this characteristic. Then we identify a simple conflict context based on probabilities within which animals may acquire, from experience, increasingly accurate information about their relative fighting abilities. This hypothetical information context relies on a few broad assumptions regarding distribution of ability within a group, and enables predictions for detailed analysis of conflict behavior based on probability of winning contests. In the following section we define and discuss the set of independent variables in addition to fighting ability that can affect the behavior and the outcome of contests. We combine these under the heading of motivation. A conceptual construct of the relationships between these variables and fighting ability is developed, and we discuss incorporating these relationships into analyses of conflict behavior. We conclude by applying predictions from the fighting ability model to various empirical examples of some commonly described patterns of animal conflict settlement such as linear dominance hierarchies, the residence effect and the outcome effect.

DETERMINANTS OF CONFLICT OUTCOMES – FIGHTING ABILITY

Fighting Ability

Resource holding potential was originally defined by Parker (1974) as absolute fighting ability, but subsequent usage of RHP varies (e.g., "inherent fighting ability" — Parker 1982; "intrinsic power" — Dunbar 1988; "the constellation of factors that influence fighting ability" — Krebs and Dawkins 1984). Usage frequently confounds extrinsic and intrinsic variables. RHP may be a dependent variable, equivalent to the probability of winning (PW; Petrie 1984; Freeman 1987), or be an independent (subject) variable describing the relationship between individual ability and the outcome of a contest, as Parker (1974) originally intended. Contrary to Parker's (1974; Maynard Smith and Parker 1976) original intention, RHP may be used simply as a label for the contest winner. This usage has little utility in analyses of the determinants of contest outcomes. Nevertheless, this alternative meaning, implied by 'resource holding potential' has become common usage. "...RHP is a measure of the capacity of an individual to hold a resource" (Maynard Smith 1982b). With this usage, the possibility that an opponent could lose a contested resource to an individual with lower RHP is counterintuitive, but that possibility was clearly considered by Maynard Smith and Parker (1976). Similarly, Dunbar's (1988; Dunbar et al. 1990) recent use of 'power' as another surrogate term for FA suffers from alternative meanings and its absence from other literature. Since RHP as currently used is inexact we find no reason to call fighting ability by any other name, and return to this earlier (e.g., Ginsberg and Allee 1942) and still widely used term. Wherever possible we have used dictionary definitions of terms to enhance the prospect for wide consideration of these concepts.

Abilities are capacities, inherited and gained by experience, to perform actions. Fighting ability is a dynamic phenotypic individual characteristic. As used here, it is the potential to prevail in physical contests against others for status, resources, and mates. We distinguish between contests involving fighting and those which do not. Fights are encounters involving attempts to defeat an opponent by physical contact. Fights usually produce winners and losers, but draws are possible. Displays, probing, sparring and other interactions are examples of contest encounters that are not fights but may include physical contact and convey information about relative FA. Limited encounters, not involving contact between contenders may also resolve access to resources. Grafen (1987) clarifies the distinction between probing behavior and fighting and its relationship to game theory models. The distinction between probing and fighting is based on differences in costs and function. The probability of winning several high-cost fights, for example, is low and can be quantitatively defined. Probing and its associated displays, for some species, has relatively low or no costs (spiders, Hammerstein and Riechert 1988) and may occur repetitively. The difference between fighting and sparring is readily distinguished, for example, in most ungulates (e.g., Estes 1969; Geist 1971, 1974; Barrette 1977; Hirth 1977; Wilson and Franklin 1985; Barrette and Vandal 1990). Among the chacma baboons we observe males display with loud calls (wahoos) repeatedly over a period of days or weeks. When a rare physical contest between these monkeys occurs the distinction between vocal sparring and its associated positional maneuvering and overt fighting is obvious. In other animals the distinction may be less obvious, as for some insects (e.g., Crespi 1986), though some contests described as fights between adult insects do have clear winners and losers (e.g., Hamilton et al. 1976; Davies 1978; Waage 1988; Marden and Waage 1990).

Differences in fighting ability between individuals are influenced by stage of development to and throughout senescence, condition and experience (Collias 1943; Parker 1974). These variables, combined with a heritable component, collectively determine the present (instantaneous) FAp (Table 1). FA may explain some, all or none of the variance in contest outcomes and access to contested resources. Abilities other than FA as, for example, foraging skills, may determine competitive potential, especially when contest competition is of limited or no importance to resource acquisition. FA is an individual characteristic which generally increases during ontogeny to some maximum individual potential, then declines as a result of costs incurred in contests and from senescence. Temporal patterns of FA vary by species and individual, both between and within populations. These variables collectively comprise the minimum set of components of fighting ability. Fighting ability contributes to the probability that opponents will enter into and persist with patterns of conflict behavior and prevail as contest

Table 1. Components of Fighting Ability and Some Examples of Factors Contributing to Them. These Positive and Negative Effects Collectively Determine an Individual's Present Fighting Ability (FAp)

- FAi (Inherited characteristics)
    - Gender
    - Adult body size
    - Other inherited morphological and functional differences between individuals
    - Behavioral traits
- FAd (Developmental state)
- FAc (Condition)
    - Current mobilizable energy
    - Slowly mobilizable energy reserves
    - Stress state
    - Conditioning (exercise)
    - Parasite effects
    - Injury effects
    - Disease effects
- FAe (Experience)
    - Acquired tactics
    - Degree of coordination of known behavior
    - Knowledge of context of effective behavior
    - Play
- FAs (Senescence)
    - Wear effects
    - Design-based declines
    - Declines in capacity to recover

winners. To determine their respective effect upon conflict behavior and contest outcomes, some components of FA can be set equal by experimentation or ordering of field observations, but empirical analyses which fail to identify a complete set of FA components may reach invalid conclusions. We find no examples in the literature on fighting behavior or from personal experience that cannot be allocated to these specific components. A review of recent literature shows that some authors consider a more or less complete set of these components (Olsson 1994; Thorpe et al. 1995). Others do not.

Inheritance (FAi)

FAi is the heritable component of differences in fighting ability. In nature FA often is measured by the outcome of contests between adults. The contribution of inherited differences between individuals to differences in performance, while conceptually straightforward, may be empirically problematic. In many animal species gender has an enduring effect upon the expression of behavior and other attributes determining conflict behavior. For some species gender may be more important than any other variable in explaining the contest outcomes (e.g., Richner 1989). All components determining FA have an inherited component including, but not limited to, some determinants of body size and behavior patterns. Individual differences between rhesus macaques (*Macaca mulatta*) in response to stressors have inherited components (Suomi 1983). Artificial selection for characteristics modifying the ability and disposition of animals to fight (Reed 1969) has been highly successful within domesticated strains of dogs, fish and birds (Darwin 1871; summarized in Huntingford and Turner 1987). The results of artificial selection in modification of contest behavior and patterns of conflict outcomes (e.g., Van de Poll et al. 1982; Thornhill and Sauer 1992) are based upon variation in heritable characteristics, some of which determine FA. Some authors refer to the inheritance of fighting ability (e.g., Rohwer 1982). More often the terms intrinsic (cf. Maynard Smith and Parker 1976; Popp and DeVore 1979; Whitfield 1987) and inherent (Parker 1982) are used, implying but usually avoiding specific statements about the contribution of inheritance. These circumlocutions and fashionable deference to current social mores dealing with the concept of inheritance of behavior in any organism have been an impediment to the development of behavioral biology as a precise science. Surrogate terms for motivation, considered below, have also contributed to vagueness and a discontinuous discourse.

Motivation to enter into and persist with encounters is determined in part by inherited characteristics (Ginsburg and Allee 1942; Barlow et al. 1986). A game theoretic approach may profitably analyze the environmental, including demographic circumstances in which alternative levels of aggressiveness succeed. Here in addition we distinguish between disposition to attack, experience notwithstanding, which we call inherent aggressiveness, and that part of aggression which has been modified by experience. Inherited dispositions may determine contest outcomes (Barlow et al. 1986). Interspecific and intraspecific differences in aggressive behavior (Ginsburg and Allee 1942; Scott and Fuller 1965; Bekoff 1974) as well as interindividual differences within a population (Thornhill and Sauer 1992) have a heritable component the characteristics of which are probably related to patterns of conflict behavior and contest outcomes.

Centuries of artificial selection for fighting performance by cock and dog breeders (Hoff 1981) has produced subjects unsuited to unqualified analyses of ESSs or other studies of the adaptive features of conflict because the aggressiveness of domestic animals is not in harmony with maximization of lifetime reproductive success except as determined by breeders. Nevertheless, strain differences and differences in aggressiveness, termed gameness by breeders of fighting stock (Finsterbusch 1980), demonstrate that inherent aggressiveness is subject to selection, independent of ability. For pit bulls (as considered here, American Staffordshire Terriers) expression of innate aggressiveness is also subject to modification by experience (Clifford et al. 1990). Elaborate apparatus and training regimens such as those which feature the preparations of fighting domestic cocks (Finsterbusch 1980) are essential to maximize the probability of winning staged contests. The expression of inherent aggressiveness is thus responsive to modification by experience in these cases gained during the training process. The results of breeding for fighting ability in domestic animals nonetheless reveal the presence of inherited controls upon thresholds for the expression of aggression modified by artificial selection. These thresholds are treated here as determinants of motivation (see below) rather than ability.

During growth, most animals avoid fights with older, larger and more experienced individuals. Inherited patterns of responses to larger opponents may discourage developing individuals (lower FAd, below) from entering encounters with individuals who could easily defeat them. A single escalated encounter against a substantially larger and/or older more experienced individual could be costly. Avoidance of contests with larger individuals, independent of experience, may prevent costly premature fights. Inherited behavior patterns of this sort may be one basis for the widespread use of displays exaggerating apparent body size. These displays are more likely to be effective against younger and inexperienced than older and more experienced opponents. It is also probable among longer-lived animals that individuals learn the punishing costs of interacting with larger individuals during development. Dogs, monkeys, rats and mice reared in isolation are more prone to attack than socialized controls (Jackson 1988), suggesting that for these relatively well-studied animals development of appropriate levels of expression of aggression in contests is in part gained by experience. Recent analyses of conflict often ignore or do not make explicit the role of inheritance in determining the range of potential responses to competitors.

Development (FAd) and Senescence (FAs)

FAd is the effect of growth and maturation to adulthood upon FA. Differences in FAd within same-age and same-sex cohorts may be relatively small compared with other parameters determining contest outcomes. However, especially among fish such as salmonids (Newman 1956; Yamagishi 1962) and cichlids (Francis 1988), FAd changes as a function of nutritional and/or social environmental conditions, largely independent of age (see also anthophorid bees, *Centris pallida*, Alcock et al. 1977; naked mole rats, *Heteromeles*, Jarvis 1978, 1981). Within a natural social grouping of competitors there are often cohorts of both sexes and of broadly different ages and degrees of development (FAD) reflecting both social organization and demography. In such groups differences in FAd are often decisive in determining access to resources.

Fighting ability typically rises to some maximum value during development, then declines. Age may be viewed as a determinant of male competitive success (e.g., Dunbar et al. 1990) but is more appropriately identified as one of its correlates (Noë 1994). While age usually closely tracks development, the relationship of age to the probability of winning also includes experience and condition (FAe and FAc, below). In empirical studies it will be useful to identify the respective contribution of these components to age-correlated differences between individuals in fighting ability. Among mammals (cf. mountain sheep, *Ovis canadensis*, Geist 1971; chimpanzees, *Pan troglodytes*, Bygott 1979; savanna baboons, *Papio* spp., Packer 1979; Dunbar 1988; Noë 1994) and birds (cf. Robinson 1986a, b; Arcese 1987, 1989) individual FA characteristically rises to some maximum value (Fig. 1) correlated, but not necessarily synchronous, with the age at which adult size is attained.

Fighting ability then declines due to losses in condition and the effects of senescence (FA), as with mechanical senescence (Finch 1990) from wing wear in damselflies, *Calopteryx maculata* (Forsyth and Montgomerie 1987). In the chacma baboons (*P. ursinus*) we study, adult males attain their maximum probability of winning contests for alpha rank at about 100 months when their upper canines reach maximum length and their probability of attaining maximum rank (Hamilton and Bulger 1990) and access to fertile females (Bulger 1993) peaks. Weight gain at high rank may add to FA and contribute to the temporary maintenance of high rank. Infrequent but serious fights with other contenders

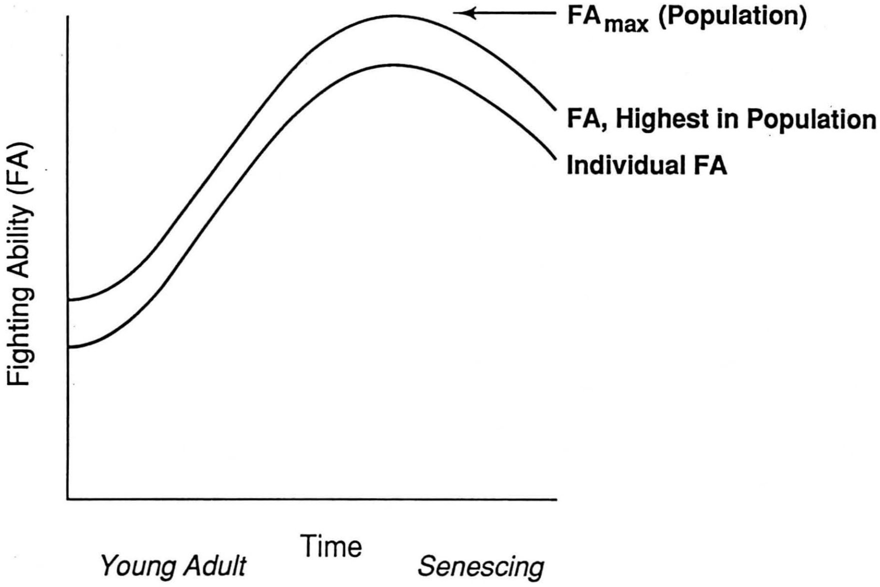

Fig. 1. The late ontogeny of fighting ability (FA), illustrating its increase to a maximum lifetime value followed by decline due to senescence (FAs) and irrecoverable losses in condition. The mean and maximum fighting ability (FAmax) for the population are identified to indicate variance from a mean and a maximum equivalent to FA = 100 in our model (pg. 195). Note that FA also varies on a shorter temporal scale from the ontogenetic trajectory owing to changes in condition (FAc) and/or experience (FAe).

may result in debilitating injuries (FAc if fully recoverable, FAs if not) including especially canine breakage. Our observations of aging adult males (>12 yrs) are few, but a general decline in capacity at this age is evident three years after males first attain alpha rank, and few males recover alpha or beta rank and access to fertile females after their first loss to a challenger. The analysis of senescence is a particularly challenging parameter to evaluate (Alexander 1987) since from the perspective of the approach advocated here it would be necessary to separate changes in condition from the cessation of increases in FAd. The relationship of FAi to FAs in Fig. 2 reflects Williams' (1957) pleiotropic theory of the evolution of senescence.

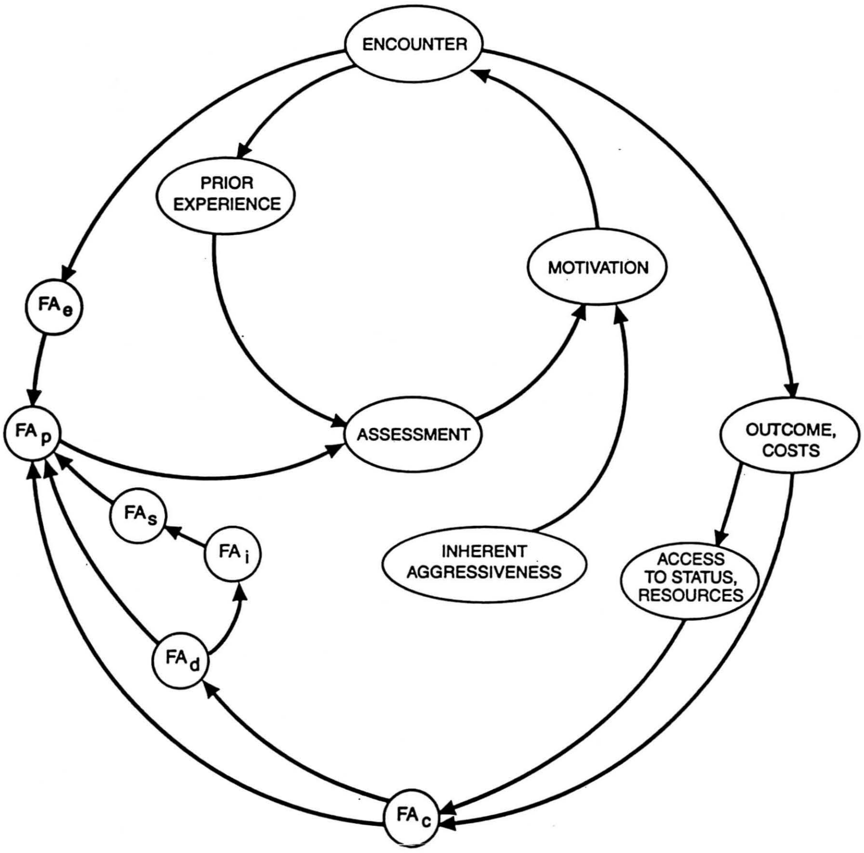

Fig. 2. Components contributing to fighting ability and their interrelationships. Additional parameters regulating aggression and providing information which might modify probabilities and patterns of contest behavior are shown in Figs. 5 and 6 below.

Body size, a commonly evaluated operational measure of FA, is not a component of FA here but we identify its contribution to several components of fighting ability. Body size has some measurable heritability (FAi, e.g., Cade 1984; Dixon and Cade 1986) but it is also an expression of development, regulated by the endocrine system, and of condition. Within some animal populations greater relative body size, measured by linear skeletal or other morphological measures (red-winged blackbirds, *Agelaius phoeniceus*, Searcy 1979; shrews, *Sorex araneus*, Barnard and Brown 1984; fish, *Salmo gairdneri*, Abbott et al. 1985) or mass (spiders, *Agelenopsis aperta,* Riechert 1978; *Euophrys parvula*, Wells 1988; frogs, *Uperoleia rugosa*, Robertson 1986), predicts contest outcomes (review in Enquist and Leimar 1983). However, within natural populations of other species, body size, however measured, often does not predict contest winners (e.g., red-winged blackbirds, Eckert and Weatherhead 1987; olive baboons, *P. anubis*, Packer and Pusey 1985; Bercovitch 1989; gelada baboons, *Theropithecus gelada*, Dunbar 1988; African elephants, *Loxodonta africana*, Poole 1989; carrion crows, *Corvus corone*, Richner 1989; velvet swimming crabs, *Necora puber*, Smith et al. 1994). The effects of body size range from slight differences accurately predicting contest outcomes (<2% by weight for cichlid fishes, *Cichlasoma citrinellum*, Barlow et al. 1986; Jakobsson et al. 1979) to the observation that substantially smaller individuals (elephants, Poole 1989a) may prevail.

Since differences in performance are not necessarily determined by body size, the relationship of body size to outcomes needs consideration within a multivariate context. Differences in body size may predict or determine contest outcomes, especially between young, less developed and older individuals, or between the sexes in sexually dimorphic species. But younger and smaller (<FAd) individuals may not be part of the contending cohort in nature (swordtail fish, *Xiphophorus helleri*, Ribowski and Franck 1993a) and their inclusion or exclusion from analyses will bias interpretations of observations toward or away from identifying size as a determinant of contest outcomes. For some species (e.g , seasonally territorial birds), resource apportionment may result from contests within large cohorts of same-age and same-sex adults, all nearly equal in body size. When such cohorts breed seasonally large numbers of mature individuals may compete for limited resources and a measurable size difference correlated with contest outcomes is not necessarily predicted.

When evaluating size as a determinant of contest outcomes some authors do not distinguish between differences due to skeletal or other morphological changes during growth (FAd) and those resulting in fluctuations in body mass about the skeletal frame (FAc, but see Olsson 1994). Mass of individuals as a measure of size and, therefore, as a predictor of FA, may explain much of the variance in contest outcomes for animals that are not resource limited, as for provisioned and captive animals. But mass or other measures of size are inadequate measures of fighting ability because they do not necessarily reflect FAc, which may be equally or more important than FAd in determining FA. Despite numerous observations that skeletal size and mass are often not closely correlated with contest outcomes, especially in seasonally breeding birds but also among adult primates, they continue to be used as operational or surrogate measures of FA (e.g., Andren 1990).

Condition (FAc)

Variation in FA due to differences in condition (FAc) may be induced by changes in nutritional state, molt status (birds, Collias 1943; crustaceans, Caldwell 1986; Adams and Caldwell 1990), levels of energy reserves (fowl, Collias 1943; spiders, Riechert 1988; African cape buffalo, *Syncerus caffer*, Prins 1989; Prins and Iason 1989), conditioning (exercise) and the effects of injuries (Packer 1979), parasitism (Sutherland and Parker 1985) and disease. FAc may change gradually or abruptly and at any age. Abrupt changes in condition may result from injury or exhaustion. Packer (1979) suggests that losses in FAc may result from the cumulative effects of injuries to olive baboons, but does not provide convincing evidence. Some losses in FAc, including some of those due to injuries and many of those due to loss of energy reserves, are fully recoverable. Other losses of FAc are permanent, especially for some injury and disease effects.

Confounding of FAd and FAc often results because of their interdependence. Among adult holometabolous insects individual differences in FA are due to the components FAd. The relationship of size to FA for emergent insects which continue to gain mass (FAc), cuticular material (FAd) and, as a result, competitive potential following eclosion (dragonflies, *Erythemis simplicicollis*, McVey 1988) reflects the phylogenetic pattern of development imposed by eclosion.

Differences between individuals in FAc which influence FA may accrue during intervals when no, or relatively little, contest competition occurs. Such changes may determine condition before animals arrive at breeding areas following migration (elephant seals, *Mirounga angustirostris*, Le Boeuf 1974; Le Boeuf and Reiter 1988; snow geese, *Chen hyperborea*, Rockwell et al. 1985), or before entering contests at the end of winter (fallow deer, *Dama dama*, Festa-Bianchet et al. 1990; moorhens, *Gallinula chloropus*, Petrie 1983; sage grouse, *Centrocercus urophasianus*, Gibson and Bradbury 1985).

Experience (FAe)

Experience may modify fighting ability by incorporating new or refining existing patterns of conflict behavior (Barash 1982). Experience may be gained during play (Groos 1898; Aldis 1975), sparring and probing (Grafen 1987) and from observation of contests between others (Freeman 1987). For example, male chacma baboons nearing maturation (>80 mos) often closely approach escalated contests by adults (>90 mos) coming so close that the encounters may appear to be triadic. However, these younger males do not participate in these contests except as close observers and probably their actions are used to gain experience through observation. FAE increases when individuals learn new fighting tactics and may continue to do so throughout an individual's lifetime. Nevertheless, at some point, individual FA will reach its maximum lifetime fighting ability (FAMAX), then decline as gains in experience do not keep pace with irremediable losses in FA from condition (FAC) and senescence (FAS), expressed in part as a slowing of the repair process following injury (Fig. 1), and in numerous other ways (Finch 1990).

Prior experience in conflict may also contribute to and modify motivation to engage in aggressive interactions through perception of one's probability of winning (Fig. 2). This relationship is the basis for the probability model for estimating relative FA from prior contest experience described below.

Summary of Fighting Ability

Individual fighting ability, as determined by the combined effects of the determinants identified above and their interactions, changes throughout an individual's lifetime. The rate of change of FA may differ with life history stage. Contests may have both negative and positive effects upon FA and its several components which also affect contest behavior (see below). The dynamic nature of FA through time has important consequences for conflict behavior. Due to continuous individual changes in FA we expect animals to reevaluate their estimate of their own FA and to change their contest behavior accordingly.

Differences in FA within a cohort of same-age and same-sex individuals are likely to be less than those among individuals who differ in age and/or sex, but it is incorrect to assume that FA is operationally equal for same-age and -sex individuals (Landau 1965). In an analysis of conflict in nature it is essential to distinguish individuals who are serious contenders for resources from those who are not (Grafen 1987). The relevance of studies of conflict to social animals in nature depends upon identification of the social and demographic composition of operationally relevant cohorts of competitors. If opponents are not same age and same sex or are otherwise not equivalents, large differences in FAd, gender or experience probably will determine contest outcomes.

Studies of conflict behavior of captive animals often pit same-age and same-sex adults against one another (Ginsburg and Allee 1942; McBride 1958; King 1965; primates, Bernstein and Gordon 1980; fish, Mosler 1985; Barlow et al. 1986; Keeley and Grant 1993). In these experiments the size of opponents is determined by the experimenter, not by demography and natural social groupings. Similarly, same-age and same-sex cohorts of domestic chickens frequently have been the subjects in investigations of dominance hierarchies (McBride 1958; King 1965; Chase 1982, 1985). These subjects are raised under relatively uniform nutritional and social conditions and the negative feedback relationship between contest outcome at resources and condition may be largely or entirely obscured by the conditions of captive management. Thus, differences between all FA components in this context with the possible exception of FAi would be expected to differ from natural social groupings of ancestral junglefowl (*Gallus gallus*). Even variance of FAi may have been modified by selection, as within poultry strains. In interactions within these breeds, individual differences in FA may be minimized or enhanced, depending upon breeding programs. Multivariate analyses of the contribution of the components of FA among such experimental cohorts may identify and emphasize determinants of conflict resolution not characteristic of or relatively unimportant to natural populations. When one or more FA components are controlled by experimental design, the effect of asymmetries in other FA components or other conflict determinants will increase. For example, we expect provisioned populations of animals, both in nature and captivity, to lose part or all of the differences between them in the expression of FAc, enhancing the probability that FAi, FAe, and FAd will determine contest outcomes.

Because the physical and experiential determinants of FA are dynamic, the contribution to contest outcomes will vary between individuals throughout their lifetimes. Feedback relationships between conflict outcomes and FA will result in varying effects of alternative parameters upon different individuals within populations. The importance of particular conflict parameters to animal populations can be elucidated by considering past and present individual circumstances, including demography of relevant social groupings. Separation of the components of fighting ability in models may present difficulties, but for empirical behavioral studies of contest outcome determinants, their separate analysis is essential before concluding, by elimination, that other parameters such as resource value and costs determine outcomes and access to resources.

PROBABILITIES OF GAINING ACCESS TO STATUS AND RESOURCES ON THE BASIS OF FIGHTING ABILITY

Among animals that contest one another for resources we know of no example for which untested behavior patterns are the sole basis for contest resolution. There appears to be no evidence demonstrating that territorial animals defeat challengers without having their fighting ability tested in the current or some previous encounter. Nor is there compelling evidence that exclusive access to contested resources is conceded to nonkin outside the context of personal ability and experience.

Throughout their lives individuals gain probabilistic information about their personal ability which can be related to the abilities of others. This

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Clutton-Brock et al. 1979; North American cervids, Geist 1986; velvet swimming crabs, Thorpe et al. 1995).

As risk increases, the probability that an individual will enter contests may decline. When risks are high, as for animals armed with morphological weapons, and V is relatively low, assessments of prospects by contestants may result in settlements without fighting (Geist 1974; Berger 1981; Rohwer 1982; Rubenstein 1982). Thus, because of high risks of fighting to some animals the effects of large asymmetries in fighting ability upon resource allocation may be partially or fully obscured. Contests settled on the basis of decisions to avoid costs may allow individuals with lower FA to gain access to resources. A comparative analysis of the risk of conflict to lions, chimpanzees and olive baboons appears to demonstrate the importance of risk in determining how contests are settled (Packer and Pusey 1985). Resource access may be determined by prior access, and settlements appear to be conventional. However, we (Hamilton and Bulger 1990) tested this possibility for immigrant male chacma baboons challenging resident paternal alpha males, but found that the success of challengers far exceeded the predicted value of about 0.5. Risky fights between adult male chacma baboons involve use of potentially lethal weapons (Hamilton and Brain, personal observations) and we conclude that resident paternal males are unwilling to accept the risks taken by immigrants with no progeny.

Social Determinants (S) of Contest Outcomes

Early game theory models avoided analysis of contests between individuals known to one another, thus avoiding the complications introduced by prior acquaintanceship (Maynard Smith 1982a). In nature contestants often are known to each other and these social relationships may be important in determining contest outcomes. In addition to the knowledge individuals have about competitors from experience following probes and fights, there are two additional ways social relationships can modify contest outcomes. Individuals may: (1) withhold the full expression of aggressive potential (concessions, Sc) and (2) support others in contests (Ss) (Table 3). Sc is the concession of resources or access to others, usually mates or kin (Vehrencamp 1983). When parents and dependent offspring interact, contest outcomes may not reflect the full potential of partici-

Table 3. Terminology Used in This Chapter to Identify Social Effects in Conflict Situations

Term	Usage	Number of interactants
FA	Personal fighting ability	dyads
Sc	Concessions to relatives, mates and friends	dyads
Ss	Support by third and additional parties	triads

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win:loss record, and c)
2:2 record. In all three
against an unknown op-
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pants because it may not be advantageous to either party to impose high costs upon the other (Parker et al. 1989). We view these self-imposed limits as aspects of motivation (Fig. 5). In some cases Sc may be the outcome of assessment, in others it may be an innate feature of species typical behavior based upon the evolutionary history of contest contexts and consequences. Ss is the intrusion of third and additional parties in support of others, producing outcomes which might be determined otherwise in dyadic contests were no third parties to intrude. We use the term Ss to refer to social support for allies, whether or not they are relatives. Social settings may also occur which suppress the expression of aggressive behavior, as that of dominant ravens (*C. corax*) at carcasses (Heinrich and Marzluff 1991) and resident territorial spotted hyenas allowing commuters through their territory uncontested (Hofer and East 1993).

When social support (Ss) is a determinant of contest outcomes (Scott and Fuller 1965; Gouzoules 1975; Vehrencamp 1979, 1983; Hand 1986; Smuts 1987; Pereira 1989; Noë 1990), it needs to be separately identified and analyzed. In some cases social partners are decisive in determining contest outcomes, obscuring the effects of individual differences in FA. This is the case for some primate coalitions (Packer 1977; Dunbar 1988; Pope 1990; reviewed by Silk 1987; modeled by Noë 1994). Among Japanese macaques (*M. fuscata*, Kawai 1965; Walters and Seyfarth 1987) and yellow baboons (*P. cynocephalus*) adult females attain their mother's rank (Hausfater et al. 1982). Thus, resource access may be largely independent of individual FA, although Dunbar (1988) suggests that individual 'power' (FA) plays a role in determining rank within and between gelada baboon (*Theropithecus gelada*) matrilines. Group size also may be a determinant of outcomes in intergroup interactions among primates (Cheney 1987) and is widely characteristic of social carnivores (lions, Bygott 1979; McComb et al. 1994; Grinnell et al. 1995; spotted hyenas, Kruuk 1972; dwarf mongooses, *Helogale parvula*, Rood 1987; African wild dogs, *Lycaon pictus*, McNutt 1996). Larger family groups of geese tend to prevail in contests over food in nonbreeding situations (Boyd 1953; Hanson 1953; Raveling 1970). Among some territorial animals (fur seals, Getty 1981, 1987; song birds, Jaeger 1981) neighbors collaborate to evict intruders, perhaps stabilizing relationships between individuals in the neighborhood. In circumstances where conflict involves numerical superiority by groups over other groups or of collaborating dyads over single individuals, social support may mask the expression of individual FA such that relatively inferior individuals (<FA) prevail in contests. In this case patterns of settlement such as early settlement, for example, where social support is provided by a neighborhood effect, may be decisive in determining contest outcomes (see below). The fighting ability of savanna baboon coalition partners may, however, be a determinant of the outcome of contests (Noë 1990) and the assessed FA of potential partners may influence their choice of coalition partners (e.g., Pereira 1989; Noë 1994). We identify this relationship between FA and Ss in Fig. 5.

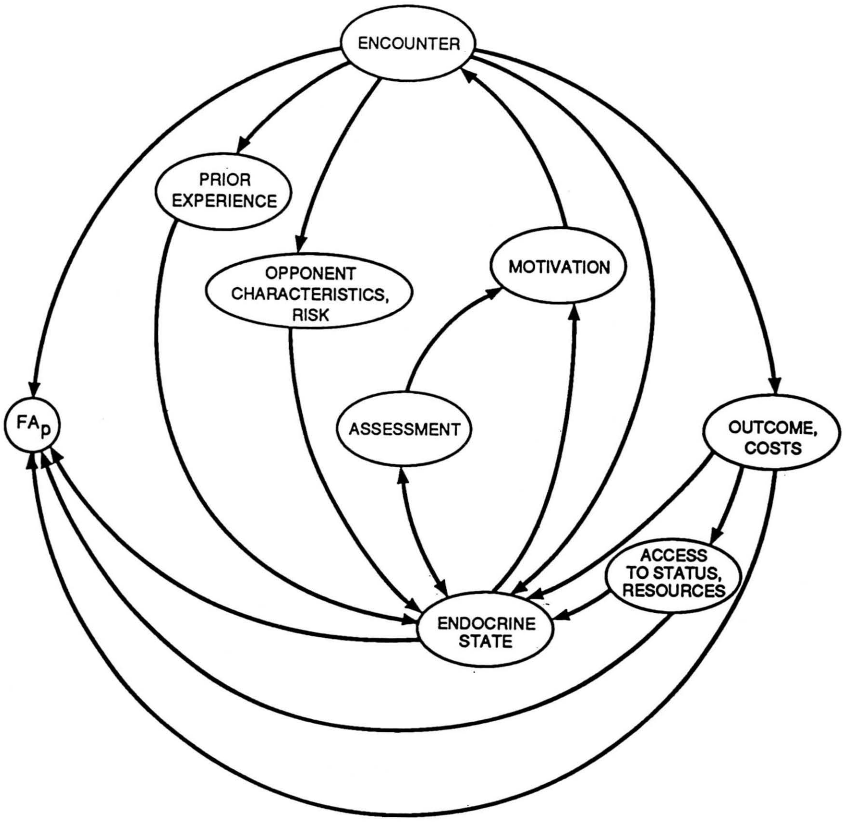

Fig. 6. Endocrine regulation of the expression of conflict. Arrows indicate a potential modifying relationship of state or status and, for motivation, probabilities and characteristics of responses.

Motivation

Motivation is defined here as willingness to engage in behavior. Many authors are at present unwilling to use the term motivation, but the array of surrogate terms such as tendencies, propensities and resource value are inadequate substitutes. Dunbar and colleagues (1990, p. 665) for example, substitute for motivation "...the extent to which a male is prepared to take on...." Excision of motivation from behavioral vocabulary and thinking has led to an ambiguity in some literature about the distinction between ability and motivation (e.g., Hand 1986). Motivation may change in response to changes in ability, but they are separable entities. In game theory the ability-motivation distinction is made between RHP (ability) and a payoff asymmetry in V. In some usage V has become a surrogate term for motivation. Motivation of participants determines when, how long and how vigorously individuals will pursue a dyadic contest they have neither won nor lost. In dyadic interactions, individuals may engage in a contest from similar or differing motivations, dispositions, or assessments of resource values. Multiple pathways leading to motivation (Fig. 5) suggest the need to evaluate outcome determinants from a multivariate perspective. Motivation may be modified by long-term associations with others, especially relatives, mates and coalition partners (Sc). The relative value of resources may add to or subtract from motivation, depending upon assessment of several parameters. Prior experience in contests, including play, sparring and previous fights provide a source of information for individuals about their probability of prevailing, which should affect motivation. Costs likely to accrue in contests also could modify motivation. Dynamic changes in motivation have been modeled by Parker and Rubenstein (1981) who note the difficulty of measuring changes in assessments of resource value (V). But motivation cannot be set equal to resource value because V, however defined, is only one of several determinants of motivation in contest behavior (Figs. 2, 5, 6).

Mobilization Responses

The timing and intensity of conflict are regulated by endocrine changes inducing changes in motivation and condition. Endocrine state changes correlated with and induced by hormones are also changes in condition (FAc). Since we wish to limit parameters insofar as possible, we include these changes within endocrine state and, if they modify ability, within FAc. Others may wish to add a term to the FA components (Table 1) to distinguish the effects of endocrine state upon contest outcomes. If so, it will be useful to distinguish between that part of the endocrine response which enhances ability and that which modifies motivation. This relationship is represented in Fig. 6 where the effect of endocrine state upon the expression of FA is noted.

Adaptations to the regulation of advantageous timing of maximum competitive ability include the following:

Endocrine Regulation. Endocrine regulation of motivation is achieved by neural and endocrine changes which may modify responsiveness in subsequent encounters and to particular challenges. These regulatory processes are tuned to seasonal opportunities for mating and modify the timing of competitive behavior (Worthman 1990; Wingfield et al. 1990).

Spatial Patterning of Movements. Building or rebuilding energy reserves may be achieved by managing one's social environment. For example, by leaving social groups, individuals can limit intraspecific competition (African cape buffalo, Prins 1989) and behavioral subordination and suppression of endocrine status (long-tailed macaques, *M. fascicularis*, van Noordwijk and van Schaik 1985; monkeys (*Saimiri sciurus*), DuMond and Hutchinson 1967).

Stress

Stress is a fundamental physiological process which can have profound consequences on contest behavior, and needs to be considered in an adaptive context. Often the suite of physiological parameters that comprise the stress response are viewed as a chronic state and a cost. The adaptive mobilization of resources through the reallocation of energy reserves to available energy has received less attention. Earlier group selection interpretations of the role of stress in the natural regulation of densities (Christian and Davis 1964) were rejected (e.g., Ricklefs 1979) but have not been replaced by adequate alternative hypotheses (but see Pianka 1988). The stress response, earlier described as the general adaptation syndrome (GAS; Selye 1971) initially increases availability of energy, resulting in prompt enhancement of performance (Sapolsky 1987). (Selye's (1971) physiological 'adaptation' term differs from adaptation in evolutionary biology.) In conflict situations, where opponents are highly competitive and have nearly equal FA, mobilization of available reserves and their conversion to available energy (Sapolsky 1987), adaptive in an evolutionary sense, changes condition (FAc) while imposing costs (Sapolsky 1987). The stress response is part of a suite of endocrine changes tuning motivation and available energy to adaptive lifetime outcomes.

Studies of the behavior and endocrinology of African elephants illustrate the limits of application of game theory to analysis of empirical conflict behavior. Male elephants undergo long-term changes in their motivation to fight (Poole 1987, 1989a), paralleling the behavioral (Poole 1987) and endocrine (Hall-Martin 1987) state of musth, which determines contest outcomes between musth and nonmusth contestants (Poole 1989a). Musth is initiated by individuals in good condition (Poole 1989b), and is correlated with high circulating testosterone levels (Hall-Martin 1987). However, prolonged periods of musth with costs of reproductive efforts, including exceptionally long treks (Hall-Martin 1987) and fights with other males (Hall-Martin 1987), result in deterioration of condition (Poole 1989a). Using game theory parameters RHP and V, Poole (1989a) interpreted her observations as a demonstration of the role of resource value (V) rather than RHP in determining contests because poorer-condition musth males prevail over nonmusth contestants (Poole 1989a). Shoehorning such detailed patterns of conflict into the limited relationships prescribed by game theory oversimplifies the already empirically achieved level of understanding. Changes in the social milieu, endocrine state and current condition all play a part in determining the motivation of elephants in contests (Poole 1987, 1989a, b). At the very least, elephant male-male conflict is too narrowly defined if the set of determinants used to analyze the behavior does not include other relatively proximate and temporally dynamic variables such as the endocrine state of the contestants.

APPLYING THE MODEL

Linear Dominance Hierarchies

There is uncertainty about the relationship of fighting ability (FA) to rank (Landau 1951) and the maintenance of linearity in hierarchies (Landau 1965; Silk 1987). Barnard and Burk (1979) treat hierarchies and their maintenance from the perspective of probable dyadic contest outcomes. Their analysis emphasizes the avoidance of contests by incompetent individuals. The relationship of numbers of individuals in hierarchies (Landau 1965; Chase 1984) to their maintenance and character has been unclear. Comparison of the FA of individuals in different linear dominance hierarchies (LDHs) has seemed impractical because ordinal rank of FA is not directly comparable to FA ranks in other hierarchies, although cardinal indices resolve this problem when outcomes are not fully linear (Boyd and Silk 1983). Use of randomly assigned FA values avoids the problem of estimating probabilities of success on the basis of rank-ordered abilities alone. To simulate the possibility of increasing rank as a function of changing social group, we make the following assumptions about LDHs:

1. There is an exact ordering of individuals by FA among group members. That is, there is a linear dominance hierarchy based upon FA. Individuals with higher FA hold higher rank.
2. The distribution of FA within a population or social group is, on the average, the same as that of neighboring populations.

The number of FA values randomly drawn from 0 to 100, as for dyadic contests above, equals the number of individuals in the group. Rank ordering of these values identifies individual ranks in LDHs. It also allows comparison of ranked individuals from one group with individuals from any other. From the results of these simulations we can address the question: What is the probability of acquiring a higher rank by joining a different group?

Given the stated assumptions, every individual has a finite probability of entering any other hierarchy at each rank, depending upon the number of individuals in that hierarchy and the FA of the contender (Fig. 7). Others have suggested that an individual might improve status in a hierarchically organized society by choosing to enter another group where weaker individuals comprise the membership (Clutton-Brock and Harvey 1976; Cheney and Seyfarth 1983; Pusey and Packer 1987). We evaluate this possibility using a group size of 10 individuals organized in an LDH on the basis of FA. By repeatedly comparing individuals from one random group with others, we simulate contests and establish the frequency that individuals can increase rank by moving to another group (a neighboring LDH). We use these frequencies to estimate PW an alpha

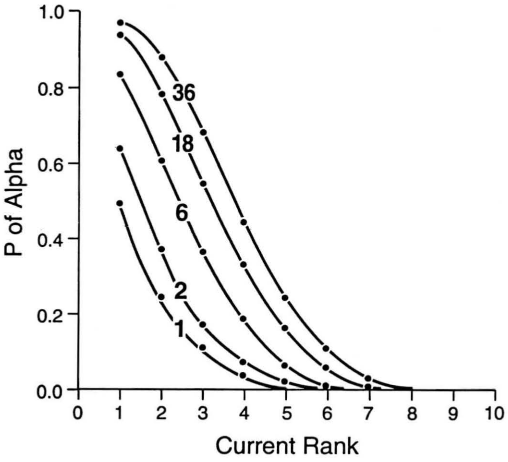

Fig. 7. The probability of an individual rising to alpha status by moving to another same-size hierarchy derived from simulations. Probability is a function of former rank (shown here for group size = 10) and number of opportunities (groups) for immigration. Ranks are based upon fighting ability (FA) and hierarchically organized groups are randomly drawn. (1) shows probability for one alternative hierarchy for initial ranks 1 - 10; (2) for two alternatives; (6) for six alternatives; (18) for 18 alternatives; and (36) for 36 alternatives.

rank elsewhere (i.e., the immigrant beats the highest rank in neighboring LDHs). The probability of an immigrant rising in rank by moving to another group is a function of its preemigration rank and the number of groups it is able to challenge. Figure 7 illustrates the increases in PW an alpha position with the number of LDHs challenged. For example, any fifth-ranking individual from a group of 10, challenging only one other LDH has a PW = 0.016 of rising to alpha status. This PW increases to 0.075 if the contestant could choose among six randomly drawn same-size groups. By comparison, a rank rise from second to first rank becomes highly probable (>0.66) if more than one group is contested. This same method will similarly identify the probability for successful entry from any rank to any other rank in variable-size hierarchies.

In practice, the increase in probability of promptly rising in rank by challenging a large number of cohorts is less than that specified by Fig. 7 because the immigrating individual may incur costs and lose FA during successive challenges. Values from the simulations show that choice of another same-size hierarchy in the same population seldom will offer more than a gain of one rank if the FA of all cohort members is independent and varies independently, i.e., if there is no social support (Ss) from other individuals during the process of rank establishment. Only immigration to a smaller group or some change in parameters other than FA determining contest outcomes will provide any substantial opportunity for rank rises by changing group affiliation. It is thus improbable that inferred substantial rank rises to alpha status by chacma baboons transferring between groups of similar size (Hamilton and Bulger 1990) can be explained by immigration into other less competitive groups. We suggest that the observations are most probably explained by differences in motivation. A choice of weaker groups is unlikely to provide a substantial gain in rank in hierarchically organized societies.

The Outcome Effect

An animal's contest behavior may reflect information about relative FA in two distinct ways: (1) how to fight (FAe) and (2) when to fight (motivation). Here we are concerned exclusively with the latter. Experience of contests won or lost may have positive or negative effects, modifying motivation and thus the probability of prevailing in subsequent contests (Ginsburg and Allee 1942; Alexander 1961; Burk 1983; Franck and Ribowski 1987, 1989; Jackson 1991; Ribowski and Franck 1993b). Such changes in motivation are not necessarily in FAE because they do not necessarily change ability. We view changes in motivation as adjustments of the criteria for deciding when to enter contests based upon perceived relative FA and an estimate of the probability of winning.

Changes in motivation in response to outcomes often involve changes in endocrine states (Baptista et al. 1987; Wingfield et al. 1987). The probabilities identified here suggest a relationship between behavior changes and correlated hormonal responses (Harding and Follett 1979; Harding 1981; Hannes et al. 1984; Wingfield et al. 1987) following changes in individual perceptions of social status (Worthman 1990), including those associated with resource ownership. When ownership of resources reflects prior contest history, i.e., that the owner has a higher FA than previous owners, contestants may behave in subsequent contests as if they had gained information about their relative FA, changes that might be correlated with, if not modulated by changes in endocrine status mediated by the central nervous system.

For many animals prior experience modifies contest behavior (Bronstein 1985; Wallen and Wojeiechowski-Metzlar 1985; Popp 1988). The consistent result of experiments in which trained or selected winners are pitted against equivalent losers in laboratory settings with same-age same-sex subjects is that consistent winners and losers behave as if they expect to win or lose subsequent contests (Ginsberg and Allee 1942; Franck and Ribowski 1987). If animals have evolved to respond to opponents on the basis of probable costs and outcomes, their current motivation will reflect these probabilities. A classical explanation for this experimentally identified prior outcome effect is that an attitude or state predicting and in part determining outcomes develops (Kahn 1951). The outcome effect, experimentally demonstrated and analyzed by psychologists, has not been incorporated into game theoretic studies. Incorporation of the fundamental probabilities of Table 2 into analyses and interpretations of conflict reconciles these earlier observations with cost/benefit analyses. Experimental demonstrations of outcome effects may result from an adaptive response to probable outcomes.

The Resident Effect

The resident effect is a corollary to the outcome effect. It is the greater than chance probability that an owner or resident will retain its residence when specific contexts, and we focus on investigating mechanisms of that behavior at the level of individual contestants. Proximate mechanisms of behavior mediate broadly flexible behavior of individuals on a temporal scale that ultimate explanations do not necessarily accommodate. Identification of parameters influencing competitive behavior has been a fundamental feature of the experimental analysis of animal behavior and the development of our current understanding of behavior, both from the perspective of evolutionary ecology and the study of mechanisms. Analyses of the determinants of behavior are proceeding effectively in disciplines which investigate complex parameters independently from game theoretic models of contests and their consequences. We find these studies to be effective in advancing our understanding of behavior and advocate a continuation of this approach to the analysis of conflict behavior. We have identified a complete set of parameters which may be used to evaluate contests even in complex contexts.

To model the relationship of fighting ability to patterns of status and resource acquisition among competing individuals, we describe frequency distributions of estimated personal FA and the resulting future probability of winning following a limited number of cost-free contests. These fundamental probabilities may pattern the behavioral responses of animals to their opponents. Costs of fighting constrain opportunities to gain experience and introduce error in matching ability and resource acquisition. We identify distribution patterns for the relationship of FA to status and tenure at resources. These probabilities provide a basis for evaluating individual conflict behavior.

Sequential interactions between opponents produce predictable frequency distributions of FA within populations which contain information about an individual's ability relative to that of other population members. Sequences of encounters result in individual win:loss records that are incorporated into an individual's experience and from which estimates of the PW in subsequent encounters can be made. Deviations from these quantitative predictions identify the degree to which other parameters (e.g., costs, risks, value asymmetries) determine outcomes. Contest strategies may be viewed as the consequences of developing and labile abilities and motivations whose components are conceptually and empirically separable. Studies of classical learning and hormonal responses (Worthman 1990) identify potential mechanisms mediating appropriate behavioral responses to probabilities of prevailing in future contests based upon information providing estimates of individual relative FA.

Analyses of conflict need to identify initial status of contestants and costs of encounters and the potential for probabilistic responses to them. It is likely that different patterns for the expression of FA components and other parameters will be found in different species and populations. Since social primates rely more upon cognition and less upon internal states in their responses to social companions, it follows that they may be able to make more externally informed assessments (Bercovitch and Goy 1990; Worthman 1990). We expect primates to be more precise and to consider more information than most other animals and so to be less constrained by prior experience and long-term states. We expect that social primates will respond in conflict situations based upon active decision making. They will assess more kinds of information than some other animals, especially those which respond reflexively, guided by comparatively few stimuli. Callithricid monkeys are more dependent upon endocrine control and less susceptible to cortical mediation than the larger primates in more complex social environments (Worthman 1990).

A probabilistic framework based upon the fundamental parameters of animal conflict combined with complete multivariate analysis of contests provides a more promising empirical approach to analysis of behavioral access to resources than paradigms which assume that FA is static or is operationally equal among competitors. Analyzing conflict behavior within the underlying context that individual decisions are based upon assessments of probable contest outcomes has broad applicability and unifies several classical behavior paradigms.

While our analysis here has been confined to fighting ability and to nonhuman animals, the relationships identified here are applicable to the analysis of all abilities, including those of humans.

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