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Animal Conflict Parameters

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INTRODUCTION

Game theory techniques were first applied to interpretations of the evolution of behavior in a model of dyadic conflict developed by Maynard Smith and Price (1973). The concept of an evolutionarily stable strategy (ESS) provided an interpretation and possible qualitative explanation for the observation that most agonistic encounters are resolved by animals without fighting or use of damaging fighting tactics. In recent years the ESS concept has emerged as a dominant paradigm in the conceptual analysis of evolutionary aspects of animal conflict.

Maynard Smith (1974), Parker (1974) and Maynard Smith and Parker (1976) provided early applications of the ESS approach to modeling conflict behavior. The assumptions of heritability and inclusion of social dynamics which were required to make the strategies evolutionarily relevant have been addressed by increasingly complex mathematical ESS models (Bishop and Cannings 1978; Riley 1979; Hammerstein 1981; Maynard Smith 1981; Parker and Rubenstein 1981; reviewed by Hines 1987).

Assumptions and simplifications subsumed by terms of ESS models appear to be based more upon mathematical tractability than upon biological relevance. Thus, despite both logical and intuitive appeal, the expectation that ESS models might provide a broadly applicable theoretical framework for empirical investigations of animal conflict remains unfulfilled.

Here we suggest an approach to the study of conflict behavior which permits empirical application of a model unconstrained by assumed conditions of population stability. In game theory jargon, we consider a population to be a set of potentially interacting individuals exhibiting a conditional strategy, aptly described as 'making the best of a bad job' (Dawkins 1980). We make two important assumptions: 1) that individuals differ in ways that can influence their success and 2) that natural selection has shaped the behavior patterns of animals to reflect fitness cost-benefit relationships (i.e., b/c > 1), as do ESS models. That alternative strategies have fitness consequences which are frequency dependent seems self evident. We assess conflict behavior by evaluating costs and benefits to the interacting individuals, rather than as population level alternative strategies. Thus, we interpret the apportionment of limited resources at the level of dyadic interactions. In this sense, the approach is antecedent to consideration of alternative strategies as a characteristic of the population.

Despite Parker's (1984) assertion that "to date most ESS theory has been of [the applied theory] type" of analysis, ESS conflict theory has led to relatively few empirical quantifications of parameters which can test predictions derived from ESS models. This is largely because quantification of fitness units, the currency of evolutionary games, must be causally linked to performance of alternative behavioral strategies in order to test predictions. Qualitative descriptions of fitness-related behavioral variability described as ESS's can be found throughout current literature. These may be appropriate for analyses of conflict with an ESS approach but they are not quantitative applications of ESS models.

There are relatively few quantitative tests of ESS model predictions about alternatives within strategy sets and those have not been entirely successful in demonstrating a quantitative fit of observations to predictions (e.g., Brockmann et al., 1979; Hammerstein and Riechert 1988). When results do not match models, the terms of the models may be adjusted (Brockmann et al., 1979; Parker and Rubenstein 1981) or additional terminology added to accommodate a range of otherwise inexplicable results (e.g., paradoxical ESSs which have no explanation but are said to account for a part of the observations; Hammerstein and Riechert 1988). When no explanation supports theory, results may be allocated to a lag in the adaptive process, with the conclusion that an ESS has not been reached (Riechert 1979) or is not attainable by the subject population due to gene flow constraints (Hammerstein and Riechert 1988). Thus, the biological significance of observations failing to match predictions from models is ambiguous, a criticism common to the general optimization approach (e.g., Gould and Lewontin 1979). It is in any case not self evident that identifying whether or not particular behavior patterns are evolutionarily stable is an important question. The uncertainty in interpretation of discrepancies between theoretical predictions and empirical observations may in part be due to constraints imposed by limiting models to broadly generalized and thus poorly defined parameters.

PARAMETERS OF CONFLICT

We suggest that studies of animal conflict behavior will be improved by re-evaluating the ESS approach, first by precisely defining relevant parameters and then by delineating in a simple causal pathway the expected relationships among these parameters. The game theoretic ESS approach has guided qualitative interpretations of conflict behavior by identifying conflict parameters for pairwise interactions (Maynard Smith 1982a). While a small set of parameters provides the elegance and heuristic value of ESS models, it also renders the models inappropriate for many quantitative and qualitative evaluations of complex behavioral interactions. Here we identify terms regularly used in ESS models and clarify their meaning by expansion to a larger set of essential terms. Evaluation of <u>all</u> of these parameters is essential for an understanding of patterns of conflict behavior in nature. In the process of reevaluation we propose abandoning a bivariate perception to conflict behavior in favor of a complex multivariate model.

Theoretical Concepts in Conflict Behavior

Most ESS conflict models are limited to two parameters: RHP (resource holding power, Parker 1974) and V (pay-off, Parker 1974; or resource value, Parker and Rubenstein 1981). The apparent applicability of ESS models to real biological circumstances is inherent in the broad nature of these parameters, which incorporate both individual ability and motivation.

RHP:

Resource holding power (RHP) was originally defined as absolute fighting ability (Parker 1974). Current usage of RHP varies by author [e.g., "inherent fighting ability" (Parker 1982); "intrinsic power" (Dunbar 1988); "the constellation of factors that influence fighting ability" (Krebs and Dawkins 1984)], including extrinsic and intrinsic parameters.

Confusion exists as to whether RHP is a dependent variable, equal to the probability of winning (Pw) (cf. Freeman 1987), or a subject (independent) variable in the relationship between an individual's abilities and the outcome of a contest, as intended (Parker 1974). If an individual has higher RHP than an opponent because it has won, then RHP is a dependent variable, presumably determined by various independent and subject variables. In this case, RHP is merely a label for the contest winner, and has little explanatory value or utility in developing predictive statements about the determinants of contest outcomes. This is clearly not what Parker (1974; Maynard Smith and Parker 1976) intended. It is, however, implied by the definition contained within the phrase 'resource holding potential', and this implied meaning has become common usage. E.g., "RHP is a measure of the capacity of an individual to hold a resource,.." (Maynard Smith 1982b). That an opponent could lose to an individual with lower RHP is contrary to a simple understanding of the term. Yet that possibility is clearly discussed by Maynard Smith and Parker (1976).

Much existing ambiguity, reflected by a failure to distinguish between independent and dependent variables, can be attributed to the early choice of the term RHP. Fighting ability (FA) is clearly an individual characteristic and thus a subject variable. The need to call fighting ability (FA) something else is not obvious, and we propose abandoning RHP in its favor.

Fighting Ability:

Relative FA may explain a significant proportion of variance observed in contest outcomes and, therefore, in access to resources. To investigate this question empirically we identify a more adequate minimum set of components of FA. As others have noted (Parker 1974; Packer and Pusey 1985), FA is determined by age, condition, and experience. These can be viewed as components which, in combination, yield the present FA (FAp). FAp usually increases during ontogeny to some maximum individual potential (FAmax) near physical maturity, then declines as a result of costs incurred in contests and senescence (Figure 1). A minimum set of variables necessary for the analysis of FA and the interpretation of individual ability in contests follows.

Inherited Component (FAi). Some authors refer to the inheritance of FA (e.g., Rowher 1982). More often the terms intrinsic (cf., Maynard Smith and Parker 1976; Popp and DeVore 1979; Whitfield 1987) and inherent (Parker 1982), are used, with specific implications about heritability remaining ambiguous. As suggested in models of intrasexual selection, heritable phenotypic characteristics of FA include body size, development of weapons such as canines, horns, antlers and talons (cf. Darwin 1871). Inherited behavioral characteristics influencing FA may also include temperament, coordination and other traits.

Growth (FAg). Parker (1974) and Maynard Smith and Parker (1976) noted that age influences the FA of interacting individuals. We use FAg to include the effects of growth, maturation to adulthood, and senescence.

For some species, FAg may be operationally subsumed by age, and it is convenient to consider FAg as a characteristic of a growth schedule. I.e., same-age individuals may have nearly equal FAg. This does not mean that FAg has no variance within SA-SX cohorts, but rather that FAg is relatively equal compared with other parameters likely to determine contest outcomes. The sequence of growth for individuals is comparable to that for circadian rhythms which, in the absence of environmental cues, run at individually characteristic rates close to but not equally different from 24 hours.

However, especially among fish such as salmonids (Newman 1956; Yamagishi 1962), FAg changes as a function of specific physical and/or social environments (see also naked mole rats, Heteromeles, Jarvis 1977; anthophorid bees (Centris pallida) Alcock, et al. 1977). Differences in FA among SA-SX individuals will often be due to a combination of other FA components (FAi, FAe, or FAc; below). Variation of FAg assumes different schedules within alternative taxa. Among mammals, individual FAg characteristically rises to some asymptote correlated with the age at which adult size is attained, then declines due to the effects of senescence and other FAc variables [Figure 1; cf., mountain sheep (Geist 1971); chimpanzees (Bygott 1979); savanna baboons (Packer 1979; Dunbar 1988)].

<Figure 1 here >

Condition (FAc). Variation in FA due to condition as used here includes differences due to nutritional state, levels of energy reserves, and the effects of injuries and disease. Thus FAc may change gradually or abruptly through time and at any age. Relatively long term FAc differences include, for example, condition upon arrival at breeding areas following migration (snow geese, Rockwell, et al. 1985) or at the end of winter for non-migratory species [moorhens (Petrie 1983); sage grouse (Gibson and Bradbury 1985)], and from debilitating injuries, [e.g., baboons (Packer 1979)]. Short term effects include energy expended in contests. Some losses in FAc, including injuries, may be fully recoverable.

In considering size as a potential determinant of contest outcomes few authors distinguish between differences due to skeletal or other morphological changes during growth (FAg) and those resulting in fluctuations in body mass about the current skeletal frame (FAc). Among adult holometabolous insects individual differences are entirely due to parameters other than the current effect of FAg. Weight of individuals as a measure of size and, therefore, as a predictor of FA, may be sufficient for animals which are not resource limited (e.g, most captive animals, see Barlow et al. 1986) but be inadequate for others for which condition may reflect current FA independent of weight.

Experience (FAe). Experience may modify FA by incorporation or refinement of patterns of conflict learned during play, in sparring, and from observation of contests between others (tactics) (e.g., Freeman 1987). We emphasize the difference between the effect of experience upon FA and upon fighting behavior. Fighting experience may have a positive effect upon tactical FA. However, experience in contests may also have a negative experiential effect upon behavior, reducing motivation and the probability of prevailing in subsequent contests (see Hamilton and McNutt 1989).

FAp. FAp is current ability, determined by the value of components. The value of FA components changes throughout the lifetime of an individual, and the rate of change may differ with life history stage. During growth, most animals avoid contests with older, larger and often more experienced individuals, confining them to other SA-SX and approximately same size (SZ) individuals. Here we distinguish between contests or fights which are earnest efforts to prevail and encounters, which may involve displays, probing, sparring, and other interactions lacking a prevailing winner. We avoid the term escalated to describe fighting because we assume that all fighting individuals are attempting to prevail. This distinction has a clear empirical basis in cervids, where the preliminaries to actual fighting have long been distinguished (Barrette 1977). FAp changes throughout an individual's lifetime as a result of development (FAg), condition determined by long term and short term food intake (FAc), injuries sustained during prior social interactions (FAc), gains from experience (FAe) and the continuing expression of FAi. Contests may have both negative and positive effects upon FAp, by reducing FAc and by increasing FAe.

Resource value (V):

The other general parameter modeled by ESS theorists is resource value (V) (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981). Like FA, V is a complex parameter lacking consistent usage in current literature. V is usually analyzed as an independent variable and is said to account for all or a part of observed outcomes. The meaning of V varies among authors. This is, in part, because of a failure to distinguish between 1) asymmetries in information about absolute value (Vabs) of the resource, as may arise between a resident and an intruder (cf., Riechert 1979; Ewald 1985; Beletsky and Orians 1987; Stamps 1987); and 2) asymmetries in the relative value (Vrel) of a resource due to differences in the residual reproductive value of the interacting individuals (Williams 1966). Large differences in Vrel as a function of short term survival, as between starved and well fed individuals, have been shown to influence contest outcomes [e.g., shrews (Barnard and Brown 1984); bald eagles (Hansen 1986)].

Because of differences in age, especially among iteroparous animals, asymmetries in Vrel based upon residual reproductive value (Williams 1966) may also determine the expression of behavior. Fitness values for V are relative to the residual reproductive value of each contestant. Effort expended in gaining or maintaining access to a resource may vary with V if it is a function of residual reproductive value [Popp and DeVore 1979; also called 'expected future reproductive success' (EFRS); Grafen 1987]. The predicted inverse relationship between reproductive effort and reproductive value has found limited empirical support (cf., Nur 1983; Clutton-Brock 1984). The same relationship is expected between V and effort in contests as with reproductive effort (e.g., parental investment), and EFRS (Fisher 1930; Trivers 1972; Pianka 1976). This relationship is generally ignored in empirical analyses and interpretations of animal conflict (but see Grafen 1987).

As EFRS approaches zero, Vrel is expected to increase and fights to the extent of individual ability, regardless of personal FA, may result ("desperado" behavior - Grafen 1987). Popp (1978) suggests that desperado-type behavior occurs among savanna baboons, but that case is equivocal. Fights to the death are rare in nature, perhaps because EFRS is seldom zero and also because the Pw a contest based upon relative FA rapidly approaches zero after a relatively small number of losses (Hamilton and McNutt 1989). Any individual who retreats reserves some non-zero EFRS, and if contest outcome is an almost certain loss and cost, the reserve strategy of avoiding contests and making gains in FA (FAc, FAe, FAg if growth and maturation are increasing) may be the better choice.

In seasonally semelparous animals [e.g., anthophorid bees (Alcock, et al. 1977), checkerspot butterflies (Davies 1978), digger wasps (Brockmann et al. 1981), marsupial mice, <u>Antechinus</u> (Cockburn and Lee 1988); spiders

(Hammerstein and Riechert 1988); opposums (S.J. Austad, pers. comm.), and anadromous salmon], the effect of EFRS on Vrel in conflict may be partially controlled, due to the fact that deferred reproduction (to another season) is not an option.

Risk:

Several authors note that risk is a relevant parameter in models of conflict behavior (Maynard Smith and Parker 1976; Hammerstein 1981; Parker and Rubenstein 1981; Rubenstein 1982; Enquist and Leimar 1983). However, it is seldom distinguished from cost (e.g., Andersson 1982). We define risk as the product of a cost (in this case of fitness losses in contests) and the probability of that cost. Risks associated with fighting behavior vary among species, populations and between and for individuals over time.

Both the costs and their probability can vary independently. Risks involved in intraspecific conflict behavior may be low in some taxa [e.g., beetles (Marden 1987; Otronen 1988), hummingbirds (Ewald 1985)], and relatively high in others [e.g., spotted hyaenas (Kruuk 1972), lions (Schaller 1972)]. Variation in risk affects both the probability of winning and entering contests. When risks are high effective evaluation by prospective contestants may settle outcomes without contests (Rohwer 1982; Rubenstein 1982). Because of the high potential cost of contests to animals with weapons or other abilities to injure their opponents, asymmetries in FA may be partially or completely obscured in high risk situations (Packer and Pusey 1985).

The inverse relationship between risk and the probability of winning (Pw) due to some other asymmetry such as FA is described by Rohwer (1982). Maynard Smith and Parker (1976) arrived at the same conclusion, although for different reasons. Maynard Smith and Parker (1976) concluded that as risk increases, the effect of asymmetries in FA and V on contest outcomes becomes negligible and Pw converges on 0.5. This is most likely for species which fight with dangerous weapons and have a high probability of inflicting costly injuries (Packer and Pusey 1985). While Vabs remains unchanged, risks have the same effect on conflict behavior as a decrease in Vabs of a resource. A perceived increase in risk is expected to decrease the likelihood an individual will enter a contest.

Social Effects (S):

Social effects modify outcomes and need consideration in interpretations of conflict behavior. ESS models often avoid analyses of contests between individuals familiar with one another (Maynard Smith 1982a). Nevertheless, social relationships often are more important than FA in determining outcomes, probability of occurrence, and character of contests.

In social settings there are two kinds of social effects upon the direct expression of FA: (1) concessions of some resources to others (mates or kin, Vehrencamp 1983) which would not be conceded if outcomes were a direct function of relative FA and (2) the intrusion effect of third parties upon encounters establishing social relationships. In some animals social relationships are decisive in determining many contest outcomes, overriding the effects of differences in FA [e.g., coalitions, (Bygott et al. 1979; Silk 1987; Dunbar 1988); family groups of geese; pairs of eagles, etc.] Among all closely studied savanna baboons (P. cynocephalus) adult females have ranks determined by their matrilineage, which are thus largely independent of FA, although Dunbar (1988) suggests that individual FA ('power' in his terminology) may play a role in determining position within and between matrilines.

Social support is often a decisive determinant of contest outcomes (Vehrencamp 1979, 1983; Hand 1986; Smuts 1987), and needs to be evaluated for contests between members of social species. Social effects upon conflict behavior may obscure individual FA components. For example, when parents and dependent offspring interact, contest outcomes cannot be predicted because, regardless of the extent of the rivalry, it usually is not advantageous to either party to impose unlimited costs upon the other. To facilitate discerning the effects of multiple components of FA on contest outcomes, animals which are known to settle conflicts dyadically, without social support, should be chosen.

Empirical Concepts in Conflict Behavior

Current ESS models deal with a variety of conflict related issues. However, answers to some of the most fundamental questions remain ambiguous. For example, 1) what individual characteristics determine the outcome of encounters?, and 2) To what extent do extrinsic factors [e.g., resource value (Vabs), S, opponent's disposition] influence contest behaviors and determine outcomes? Failure to provide empirical answers to these questions may, at least in part, be attributed to a tendency to oversimplify potentially complex interactions among intrinsic and extrinsic variables. Vague terms have been used which lack conceptual and experimental control of the stated parameters. To interpret observations of contests all potential variables (FAi, FAe, FAc, FAg, S, V, EFRS, Risk) need evaluation.

Causal model:

We suggest conceptualizing interactions of the variables described above in a multivariate causal model. Figure 2 is a schematic path diagram representing these variables using path analysis conventions (Li 1975). Values and their significance will vary among species and individuals and for individuals over time. The diagram is hypothetical and qualitative, but illustrates direct and indirect relationships between variables. For example, behavior is directly affected by FAp, Risk, Value and Cost, and indirectly affected by EFRS, Cost, S, and FAp through direct effects on Risk, etc. Variables presented may have additional exogenous causes not shown.

<Figure 2 here>

The dependent variable we call conflict behavior is a measure of the motivation or disposition of an individual to engage in conflict. This may depend on the resource but is independent of the opponent. Assessment of an opponent's ability and disposition may also influence an individual's conflict behavior, but is not considered here (see Hamilton and McNutt, in press). The value of all of these parameters and their relationships to one another are subject to measurement. Operationally, conflict behavior may be measured qualitatively as 'fight' or 'not fight' or be measured more quantitatively for losers by duration (e.g., Enquist, et al. 1985; Waage 1988; Wells 1988). The direction of each causal relationship is indicated in the diagram. These are interpreted qualitatively; e.g., as FAp increases risk decreases [-] and conflict behavior increases [+]; as cost increases the probability of conflict behavior decreases [-]; etc. The relationships identified in Figure 1 will be best represented by multiple regression equations. Attempts to analyze conflict behavior from a bivariate perspective will be inconclusive because of potential masking of direct effects by interaction or suppression of variables in complex multivariate systems. Identification of correlative relationships in the causal path diagram is facilitated using path analysis.

While we use examples from various taxa to identify the relevance of parameters of conflict to a general analysis, we find unsatisfactory the practice of citing several studies pursued under varied conditions to establish the importance of specific parameters. It is likely that quite different patterns for expression of FA will be found in various species and even between populations of the same species, and that their respective importance will depend upon the relative value of other parameters.

Fighting Ability and Behavior:

A fundamental assumption of optimization models, including ESS models, is that behavior is adjusted to ability by natural selection. The distinction between fighting ability and fighting behavior is discussed by others (Maynard Smith 1982b; Popp 1978; Enquist and Leimar 1983). The following two questions clarify the distinction between behavior and ability in animal conflict: when is an individual expected to fight?, and when is it expected to win? While these are closely related issues, conflict models (Parker and Rubenstein 1981; Hammerstein 1981) may obscure the distinction. Here we address only the first question. The second is discussed in Hamilton and McNutt (1989).

In game theory models the question of when fighting occurs is addressed in explanations of "escalated contests". These usually depend on errors or imperfect information in assessment (e.g., Maynard Smith and Parker 1976; Parker and Rubenstein 1981). Escalation is another concept which begs clarification. While 'escalated contest' implies an undefined scale of intensity it frequently refers to duration. These are two distinct but important contest characteristics.

The difference between fighting and sparring seems well established in analyses of ungulate behavior (e.g., Geist 1972; Barrette 1977), but is less clear in insects (e.g., Crespi 1986; Waage 1988). A fight, by our definition, is characterized by a physical interaction in which there is an earnest attempt to prevail. Sparring, by comparison, appears to have a pre-fight function in assessment of opponents and is of lower intensity. Thus, escalation refers to a level of intensity of a contest. In this sense, display characterizes a contest of lower intensity and a fight an escalated contest (i.e., escalated to the fighting stage). Since fighting itself is a level of contest intensity, 'escalated fight' (e.g., Caryl 1981; Crespi 1986) has no additional meaning. Similarly, duration of a fight reflects nothing of the level of intensity. A long fight is not an 'escalated fight' but a protracted fight which likely reflects the comparable fighting abilities of the opponents (cf. Hammerstein 1981; Parker and Rubenstein 1981).

The relationship between ability and behavior is illustrated in our path diagram (Figure 2). Ability, especially perception of personal ability from past experience (FAe) (Leimar and Enquist 1984; Hamilton and McNutt 1989) may have direct causal relationships to behavior. The model deals with the question of when an individual is expected to fight and also illustrates the potential causal relationship between ability and the behavior. Since fighting is a dyadic interaction, two fighting individuals will have engaged in the dispute from similar dispositions (i.e., to fight for the contested resource). However, it may be important that there are multiple pathways to arrive at the same behavior complicating the issue of the probability of winning for a given individual.

Body size:

For many animals, body size, measured by linear skeletal or other morphological measures [redwing blackbirds (Searcy 1979; Eckert and Weatherhead 1987a); shrews (Barnard and Brown 1984); fish (Abbott et al. 1985)] or by mass [spiders, (Riechert 1978; Wells 1988); frogs, (Robertson 1986)], is a good predictor of contest outcomes (review in Enquist and Leimar 1983). That physically larger individuals should tend to prevail (cf. 'power', Dunbar (1988)), is a frequent but by no means universal observation. Body size does not always explain observed winners in natural contests [e.g., redwing blackbirds (Eckert and Weatherhead 1987b); savanna baboons (Packer and Pusey 1985; Dunbar 1988; Hamilton et al., 1986)]. Effects range from small differences which still predict contest outcomes [(<2%) cichlids, Barlow et al. 1986; Jakobsson 1979] to observations that individuals a fraction the size of opponents can win with social support [e.g.,young baboons with maternal support (Hausfater et al. 1982)]. Not surprisingly, disparate conclusions result from different conflict contexts which need identification. These may in fact reflect real differences between the organisms or they may demonstrate the need to consider the measures of body size within the multivariate context of conflict described above.

Body size is not a parameter in our analysis, because it is an emergent property of several FA components (i.e., FAi, FAc and FAg). In order to evaluate reports of the effect body size in conflict outcomes, it will be valuable to make the distinction. Differences in body size consistently predict contest outcomes for some animal populations, especially between young, less developed and older individuals or between different sex individuals of sexually dimorphic species. But for some species (e.g., seasonally territorial birds), resource apportionment may result from contests within much larger cohorts of biological equivalents such as SA-SX adults. It is not obvious whether we should expect to find a measurable size difference which determines the outcome of contests among such contestants. In this case it will be especially useful to evaluate all FA components, particularly recent contest experience (Hamilton and McNutt 1989).

The conclusion that FA is operationally equal for SA-SX individuals (cf., Landau 1965) is debatable. It is certainly likely to be true that the variance in FA among SA-SX is less than that among different age/sex individuals. But the arbitrary choice of the magnitude of variance sufficient for natural selection to operate is debatable. It is important to differentiate between animals which typically contest resources with SA-SX opponents in nature from those that do not. Interpretation of the results from studies of conflict depends upon identification of the natural social and demographic age-structure of potentially interacting individuals. If the subjects are not SA-SX individuals, or otherwise biological equivalents, then large differences in FAg may well explain the results. For example, assuming no social support, size will accurately predict the winner between a four-year-old male red deer and a nine-year-old male. But among breeding adults size may predict few contest outcomes. If experimental subjects are SA-SX the relevance to natural social interactions, if any, must be identified.

In many captive studies of conflict behavior SA-SX adults are used to compete with one another (Ginsburg and Allee 1942; King 1965; Bernstein and Gordon 1980; Mosler 1984; Barlow et al. 1986). In these studies size may be indirectly controlled and may predict little or none of the variation in contest outcomes. In investigations of dominance hierarchies (King 1965; Chase 1983, 1985) SA-SX domestic chickens are often the subjects. These subjects are raised under the same nutritional and social conditions (i.e., no prior experience). Thus, all FA components which might be expected to vary in natural social groupings of chickens (junglefowl) (FAg, FAc, and FAe) are controlled insofar as reasonably possible except for FAi, the variance of which also may have been reduced by artificial selection of poultry. In interactions of this type, differences in FA may be minimized and the bases for settlement may reach novel solutions not commonplace in nature. As FA components equilibrate or are controlled in experimental management, other asymmetries are likely to emerge as determinants of contest outcomes. For example, FAc may be minimized in provisioned populations relative to unprovisioned same size populations, enhancing the probability that other parameters will prevail. We expect provisioned populations of animals, including experimental cohorts, to lose part or all of the expression of FAc due to otherwise naturally occurring food limitations. Equilibration of FAc may enhance the probability that FAi, FAe and FAg will determine contest outcomes. The meaning of outcomes of contests between individuals in such cohorts to the establishment of access to mates and other resources in the subject species may not be elucidated or indeed be approachable.

Risk

When the probability of incurring injury is high, conflict outcomes may be determined by prior access (lions; Packer and Pusey 1985), and conflict settlements may appear to be conventional. Identification of conventions depends upon the ability to evaluate the relative importance of risks to interacting individuals. A comparative analysis of risk by Packer and Pusey (1985), for lions, chimpanzees and baboons, seems to identify the relative importance of risk in determining contest outcomes for these species. They report observations which support the position that some conflicts are settled based upon decisions to avoid risks, i.e., to allow individuals with demonstrably lower FA to gain access to resources. This tends to be more likely in animals with relatively greater risk (i.e., lions > baboons > chimpanzees). Such a relationship seems improbable if access includes conceptive mates. To accurately assess the decision not to fight for a resource because of risk we need an accurate measure of risk in terms of fitness and the fitness consequences of conceding.

SUMMARY

Agonistic encounters and contests are the outcome of competition with direct consequences for the apportionment of resources. Evolutionarily oriented analyses of conflict behavior patterns assume that such behavior is the product of an evolutionary past.

Application of game theory to conflict behavior, introduced by Maynard Smith and Price (1973), has provided insights about alternative strategies for optimizing fitness pay-offs. Their concept of the evolutionary stable strategy (ESS) has become a standard feature of the analysis of current ecological and behavioral studies. Statements asserting demonstration of ESS's appear to lend support to the validity of these models, or the model to particular interpretations of observations of naturally occurring conflict. But the concept of an ESS is seldom well understood by empiricists and its usage as an analytic tool often obscures analyses of alternative interpretations of conflict. There are thus problems both with ESS models as they apply to complex biological systems and with their specific application.

We have identified essential components of FA; development (FAg), experience (FAe), inherited characteristics (FAi) and condition (FAc). These parameters in combination establish the present fighting ability (FAp). Social relationships (S) may modify the probability and polarity of contest outcomes, often masking the role of individual ability in determining outcomes. Additional parameters, including risk and reproductive value or expected future reproductive success (EFRS, Grafen 1987), also need to be considered in interpretations of conflict behavior.

Data essential for evaluation of the relevance of the components of FA and other parameters, which may be bases for animal decision making, include:

1. Identification of life tables in natural (evolutionarily relevant)

settings; 2. Observation of all contests for limited resources, including outcomes, and the identity of individuals involved; 3. Knowledge of the age of participants, which must be exact in those cases where FA closely tracks growth (FAg); 4. Operational measures of condition as well as size/mass measures must be identified. Mass and/or skeletal size cannot be expected to entirely explain contest outcomes; 5. Identification of individual participation by third or additional parties in determining the basis for encounter resolution (S); and 6. A measure of costs of contests, including both energy and injuries.

Use of such measures in analyses suggests a reorientation of analytic methods. To identify the determinants of contest outcomes persistent observations and repeated measures of subjects are needed. Persistent study of individuals whose social relationship to all other individuals they contact is essential if we wish to identify the determinants of contest outcomes. We note in particular Riechert's observations of spiders (1979; and Hammerstein and Riechert 1988) and Smith's (1976, 1984, 1987) studies of small birds as examples of successful investigations of relevant contest parameters in demographically relevant environments. The tracking of individual participants in field settings has only occasionally been achieved (e.g., Robinson 1988; Smith 1978, 1984).

No precise analysis of the relationship of individual abilities to contest oucomes is possible without clearly separating fighting ability into its intrinsic components. Partitioning of the components of FA, and evaluation of all the conflict parameters as suggested here is one alternative to current game theory usage, which is too broad and imprecise to be an operational guide. We acknowledge that the extensive intrusion of social relationships (Hand 1986) into analyses of conflict outcomes may obscure the relationships of intrinsic abilities to contest outcomes. We treat social determinants of contest outcomes as an important but yet unexplored parameter.

The physical and experiential features of FA are dynamic. When considered as such it is apparent that the contribution of the several parameters of conflict to outcomes will vary among individuals throughout their lives. Feedback relationships between conflict outcomes and FA will result in varying effects of alternative parameters upon individuals within populations. General statements about the importance of particular parameters can be elucidated only by a consideration of the past, present and probable future individual circumstances.

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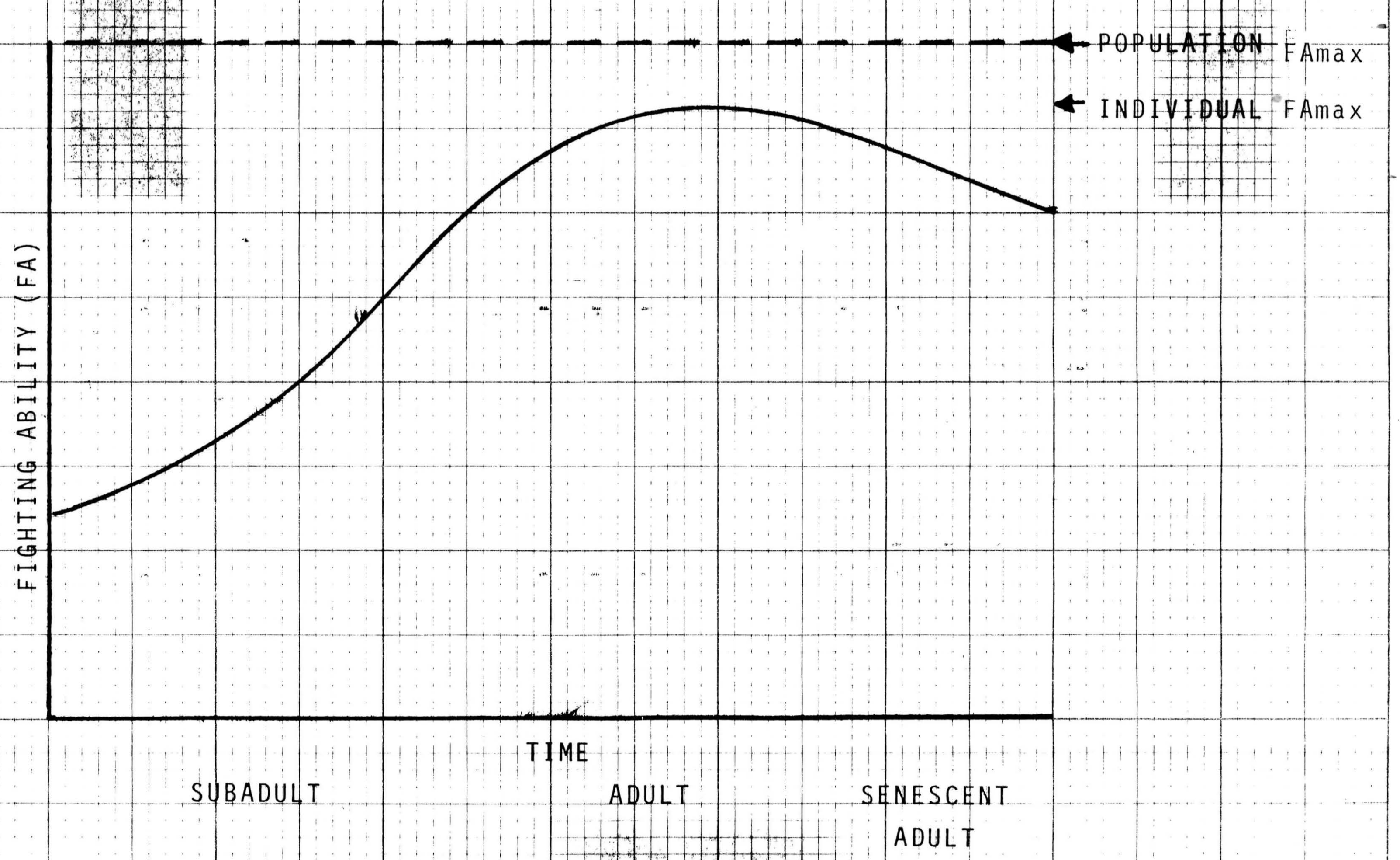

Figure 1. The late ontogeny of potential fighting ability (FA) of an individual. FA may vary at any time as a result of changes in condition (FAc), and is constrained by physical development (FAg) and inherited characteristics (FAi). Maximum fighting ability (FAmax) will vary among members of the population.

Figure 2. Conceptual path diagram of causal relationships of conflict parameters. FAp is current fighting ability, EFRS is expected future reproductive success, S is the bias in outcome induced by social others. For further explanation, see text.