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Fighting Ability and the Probability of Gaining Access to Status and Resources

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Introduction

An essential part of any interpretation of unequal ownership of contested resources is the analysis of individual competitive abilities. Here we analyze one such ability, fighting ability. Differences in fighting ability (FA) account for part of the variance in mating success, especially among polygynous mammals (Darwin 1871; Geist 1971, 1974; Clutton-Brock et al. 1979). But the relationship of FA and fighting behavior (also called combat, aggression, conflict, contest, and agonistic behavior) to the acquisition of resources with less direct fitness consequences is less obvious. Models of conflict behavior patterns usually incorporate both FA and resource value (V) as determinant variables (Maynard Smith and Parker 1976; Parker and Rubenstein 1981; Enquist and Leimar 1987). Others suggest that FA may be equal or unimportant in determining the outcome of contests among adult same age-same sex (SA-SX) individuals (Landau 1965; Barlow et al. 1986). Attempts to analyze fitness benefits as a function of V, ceterus paribus, both theoretically (Blurton-Jones 1984) and empirically (Barnard and Brown 1984) may fail to fully interpret observed relationships without incorporating differences in individual ability. Proximate and ultimate relationships of individual differences in ability to resource acquisition remain unresolved. Here we model the extent to which FA may explain patterns of contest behavior and resulting resource distribution among competing individuals, an approach modeled elsewhere only by Leimar and Enquist (1984).

It is often assumed that animals do not compete with opponents to the limits of their ability, instead substituting conventional, ritualized or otherwise limited aggressive behavior (e.g., Hingston 1933; Wynne-Edwards 1961; Maynard Smith and Price 1973; Davies 1978). We agree that most agonistic encounters are settled without contact between opponents. It is the basis of these settlements which is at issue. The conclusion that costs limit the number and intensity of contests is well established (Geist 1971; Parker 1974; Barnard and Burk 1979; Clutton-Brock et al. 1979; Abbott et al. 1985). This is especially apparent for contests between opponents with broadly disparate abilities. It seems improbable that contests which result in net fitness gains or losses are settled by conventions outside the context of current FA (as are "uncorrelated asymmetries" - Maynard Smith and Parker 1976). Respect for ownership may be an important factor in the settlement of disputes only if owners have substantially greater FA (Grafen 1987).

An ideal distribution (Fretwell and Lucas 1970) of resources to FA, with individuals with higher FA having proportionately greater access to resources, can be achieved in at least two ways. Opponents may assort themselves with respect to limited resources on the basis of an a priori knowledge of FA (i.e., without fighting), or they may have no information about their relative competitive ability when they meet and determine access to resources by observation or fighting. We offer a model which suggests how features of both these responses may be generated based upon past and future probable outcomes, regardless of how information is obtained.

We emphasize the probabilistic nature of an animal's perception of themselves relative to their environment. Acquisition of limited information during contests has previously been incorporated into the analysis of fighting behavior in the context of ESS models (Parker and Rubenstein 1981; Enquist and Leimar 1983, 1987; all accounts of the war of attrition). Here we describe how information may become available to competitors at resources from their direct or indirect experience with contest outcomes. Our analysis offers an explanation for the nearly ubiquitous observation of apparent limited fighting and the existence of conventional settlements over access to contested resources. We view conventions as behaviors reflecting decisions made on the basis of assessments and estimations of the probability of winning (Pw).

Competitive interactions are simplified here by assuming that greater relative FA determines which contestant will control a resource. Sequential interactions between opponents result in individual win:loss records. These outcomes become a part of individual experience from which information about the Pw subsequent encounters may be derived. Sequential encounters produce predictable frequency distributions of FA which have probabilistic information about an individual's ability relative to that of other population members. We suggest how animals might behave if they used this information to estimate and then effectively adjust their behavior. This analysis suggests that a probabilistic analysis of differences in FA among interacting individuals may provide insights about general patterns of contested access to resources. We apply the analysis to dyadic interactions, as in resident-intruder interactions and to linear dominance hierarchies.

Simulations: Fighting Ability and the Probability of Winning

To identify the distribution of relative FA in simulated cohorts we draw random numbers from 0 to 100, 100 representing the greatest FA for any individual. Use of the limits 0 to 100 avoids the need to consider absolute FA or to identify a specific distribution of FA values within groups or populations. Since these simulated values are percentiles they are applicable to any distribution of FA regardless of the range or distribution of actual differences. The percentile scale in some simulations is divided into 101 parts to establish 50 as a midpoint. The probabilities for a sequential loser of winning contests, based upon varying prior contest histories of both opponents, were estimated from Monte Carlo simulations and are presented in Table 1. Outcomes may provide information to both contestants, not only about their FA relative to that of a specific opponent but also relative to the rest of the field of prospective opponents.

Table 1 here

Dyadic Contests

Dyadic contests are simulated given the following assumptions:

1. All individuals have a different FA whose relative value lies within a bounded range arbitrarily set between 0 and 100.
2. Contests take place between two individuals over limited resources.
3. Greater relative FA determines the contest winner.

We simulate for all win:loss combinations from zero to 10. All contests between individuals with each win:loss record were run independently. For example, an individual with a 0:2 record is the loser of two contests (with no wins) in a group of three individuals, each drawn randomly and with each individual fighting every other individual once. Since greater FA determines contest winners, this is the equivalent of ordering the three randomly drawn individuals according to their FA, then selecting the third ranked individual. To contest against winners with 2:0 records, three more individuals are drawn at random, ranked, and the 0:2 individual then compared with the FA of the 2:0 individual. The frequency with which 0:2 wins against 2:0 following multiple interactions is the estimated Pw. This was repeated for each of the contests specified in Table 1.

If animals are responsive to or behave as if they are sensitive to information about probabilities in Table 1 when contending with one another for resources, then patterns of conflict behavior may reflect these probabilities of winning. Some general patterns may emerge from this hypothetical cue to outcome probability. These are discussed below:

I. Individuals may have no knowledge of their own FA relative to an infinite field except that which they gain from experience. Yet after each encounter they may gain an increasingly accurate estimate of their FA. For any contestant information and experience about personal FA and the Pw is gained from the won:lost record. This information often will include the identity of individuals it has defeated or by whom it has been defeated. Individuals with no prior experience and who have no information about the experience of an opponent have a best estimated Pw of 0.5. After any contest, however, the probability changes (Table 1). A one-time loser can expect only a 1/3 chance of winning the next contest against an unknown opponent. The Pw is 2/3 for the winner (Slater 1986, based upon the same logic). The Pw for successive losers is predictable and, for individuals with no prior contest record encountering similarly inexperienced others, is 1/2, 1/3, 1/4.... for successive contests. The odds for consecutive losers against successive winners is 1/2, 1/6, 1/20, 1/62.5... etc. (Table 1). A mixed record of wins and losses will yield some intermediate future Pw (Figure 1), which can be precisely stated.

Figure 1 Here

The precision of estimates of Pw in contests for resources can be improved if the win:loss record of opponents is known, even in the absence of a personal record of contests (no wins and no losses; 0:0). Contest outcomes and other information narrows the variance of perceived personal ability (Figure 2). Observation of a win by a prospective opponent predicts a lower Pw for an inexperienced observer against the winner and a higher Pw against the loser. Slater (1986) makes this argument as an alternative to Chase's (1985) interpretation of initial patterns of aggressive encounter outcomes among triads of chickens.

Figure 2 here

II. There is a predictable error in the degree of correspondence between individual ability and realized access to contested resources. This error is a function of both determinant and probable (risks) contest costs, which limit the number of contests and thus the availability of information to competitors. If dyadic contests are determined by relative FA, ownership of resources in successive encounters will increasingly agree with the distribution of FA among competitors. The extent of error from the ideal distribution is a function of the number of contests, which will in turn be a function of the fitness costs of those contests.

III. The modeled results are compatible with the observation that injurious fights between individual animals capable of imposing costs upon one another are infrequent. A decision to fight for resources or to eschew a contest may reflect both an estimate of Pw and the cost of fighting. Even if an individual has a relatively low FA it usually will have some non-zero future Pw and some expected future reproductive success (EFRS). For losers the Pw is reduced in successive encounters because, in addition to lowering an individual's estimate of its relative FA, contests may have FA-reducing costs (Guhl and Allee 1944; Maynard Smith 1974; Jaeger 1981; Grafen 1987). Without costs, fighting would continue irrespective of Pw, constrained only by time [e.g., tenebrionid beetles (Marden 1987), horned bettles (Otronen 1988) and personal observations of Namib Desert adesmine tenebrionids]. For most animals, fighting has costs for both contestants, and on the average, these may be greater for losers than for winners (Barlow et al. 1986, for captive fish; Jaeger 1981, for an experimental population of captive salamanders). Costs may include injuries and/or losses of condition and, therefore, of FA, further reducing the relative Pw of losers in future contests.

Because losers have lower average FA than winners and contests have some fitness cost, we expect losers to assess their ability and to avoid further highly likely defeats. Thus, there will be some estimated personal FA threshold below which individuals would not be expected to engage in further contests until their ability or social conditions (weakened or fewer opponents) improves. The FA corresponding to this threshold will depend upon the distribution of resources and the proportion of competitors excluded from resources. Confirmed losers with low personal estimates of their ability may thus appear to be choosing conventional settlements of encounters because their behavior accurately reflects their estimate of their Pw. A limited series of costly fights are likely to promptly settle respective tenure at resources. Subsequent interactions at resources may thus appear as conventional settlements.

Experience effects:

If individuals derive information from direct contest experience and from observation of contests involving prospective and past opponents, contest behavior patterns will reflect the Pw as a function of all relevant information gained. This experience may be reflected in an animal's contest behavior in two distinct forms: (1) how to fight (tactics) and (2) when to fight, based upon information about personal relative FA. Here we are concerned exclusively with the latter. We assume that tactics are subsumed within the term FA and, for purposes of our simulations, do not vary.

For many animals prior experience modifies the probable outcome of future contests (Ginsburg and Allee 1942; recently summarized by Frank and Ribowski 1987). The mechanism(s) involved with mediation of such apparent motivational changes in response to outcomes includes endocrine responses (cf. Bernstein et al. 1988; Wingfield et al. 1987). Probabilities identified here suggest an ultimate explanation for the observation of 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 including resource ownership. If ownership of resources reflects prior contest history (i.e., that the owner has a higher FA than another contestant) subsequent contestants are expected to act according to information about their probable relative FA and their assessment of alternatives. This decision may be based upon assessment or upon inherited responses, determined by such probabilistic information. Behavior of competitors is expected to reflect their respective Pw and their current relative status. If parameters other than, or in addition to, body size such as condition, experience or inherited characteristics determine relative FA (see McNutt and Hamilton 1989), the interpretation of observations in nature favoring wins by residents cannot be adequately evaluated unless prior contest history is known.

Wins and losses are often examined from the perspective of their positive and negative feedback relationship to future outcomes (Ginsberg and Allee 1942; Kahn 1951). The consistent result of these experiments, in laboratory settings with SA-SX subjects, is to identify an outcome effect, with winners and losers behaving as if they expect to win or to lose contests respectively (Frank and Ribowski 1987). A classical explanation for this effect is that an attitude or state predicting outcomes develops. Incorporation of the fundamental probabilities identified in this paper into analyses and interpretations of conflict may provide a reconciliation between this attitude-based and adaptive hypotheses concerned with responses to prior victories and defeats. It is possible that the experimental creation of an outcome effect simply demonstrates the adoptive response to outcomes in nature.

The Resident Effect:

The resident effect is the enhanced probability that the owner or resident will retain a residence when challenged by an intruder (Davies 1978; Barnard and Brown 1982; Krebs 1984). The residence effect appears to be a feature of most animal contests and may have the same basis as the outcome effect.

To simulate a resident effect we simulate a series of contests between all population members based upon FA and 50% resource availability (i.e., half of all contestants are excluded from residences). The initial round matches randomly drawn contestants against one another, producing half winners (residents) and half losers (nonresidents). After this first round on the average 2/3 of all eventual winners are situated at resources they will hold after N contests. If losers randomly select some resident to challenge in the next round their average Pw is 1/6. Probabilities for successive rounds are expressed graphically in Figure 3. The area between the first and Nth rounds identifies the probabilities of improving or losing status in successive rounds. In a competitive arena where there may be hundreds of individuals competing for residences (e.g., territories), a first round of encounters will produce some winners with low FA and some losers with high FA. Some losers will regain residence status in ensuing rounds. As additional contests follow, whether synchronously or separately, residences will come increasingly to be held by individuals with a competitive ability adequate to sustain their continued presence as long as they maintain their FA (Figure 3). The prospects for nonresidents will continue to dim, increasingly so because of the direct costs of losses (energy expended, injuries sustained) and indirect costs of not gaining access to resources. Thus, the model generates residence and outcome effects based upon individual relative FA and prior contest experience.

Figure 3 here

If FA is the basis for resolution of contest outcomes and if there is an ideal distribution of resources to individual ability (Fretwell and Lucas 1970) the FA of residents as modeled will equal the proportion of residents in the population. If, for example, 50% of the physically mature population are nonbreeders (as observed by Smith [1976] for the cape sparrow Zonotrichia capensis, and 52% by Jenkins et al. [1967] for red grouse [Lagopus l. scoticus]) the initial probability of establishing a territory (not an existing condition in a resident population as for Smith's [1976] cape sparrows) is 0.5 and the FA necessary to gain and retain a territory (as modeled in Figure 3) is 50. With other ratios of floaters to residents, other probabilities for initial settlement of individuals by FA on residences and their subsequent reassortment of status follow (Figure 4). The extent of correspondence between FA and residence is unknown for any study. For red grouse, contests in the fall determine which individuals will hold territories the following spring (Watson and Moss 1970). In cape sparrows, nonresidents rank themselves hierarchically, and the highest ranking local nonresidents fill breeding site vacancies (Smith 1976). If FA determines rank in these hierarchies, (as we suggest for linear dominance hierarchies, below), resident cape sparrows are individuals with relatively high FA.

Figure 4 here

In redwinged blackbirds (Agelaius phoeniceus) reversals between resident and floater status take place during the breeding season (Eckert and Weatherhead 1987). To agree with an interpretation of residence status based upon FA, some within season change in the relative FA of these opponents is implied. These could include: (1) a loss in condition of the replaced residents and/or; (2) a gain in condition or experience by prior losers during the breeding season. Collectively, observations of redwings suggest that outcomes are indeed largely determined by condition and/or experience (Searcy 1979). Eckert and Weatherhead (1987) found that in one redwing population floaters were morphologically indistinguishable from residents. But the suggestion that ownership may be based upon condition is not supported by Rohwer's (1982) experiments attempting to control for differences in condition by measuring contest success with redwings fed *ad lib*. Territory holders so tested were competitively superior to replacements (0.75). The predicted frequency derived from a probabilistic interpretation based upon FA is 0.83 for one-time contest winners, assuming that they won once against an untested opponent and that the loser lost under the same conditions (from Table 1). The actual win-loss experience of the subjects, which would make a specific prediction, was not reported.

A failure to find a correlation between morphological characteristics and outcomes is not evidence that FA does not determine outcomes. Crucial contests for resources often take place among individuals who are at or near the greatest FA they ever will achieve. Such individuals, contesting one another, are expected to be nearly equal in their ability (e.g., Jones 1987). Maximum FA is likely to be attained in the asymptotic part of the development curve. There may thus be subequal FA values for SA-SX individuals. We expect this relationship and the exclusion of uncompetitive individuals from the competitive arena to often obscure measurable morphological differences contributing to differences in FA. We thus expect that it will be difficult to identify attributes which determine FA, which may often not be morphological.

One of the conditions of our model is that no two individuals have the same FA. However, given the dynamic nature of FA it follows that two individuals occasionally must have identical FA because the curves for FA for some individuals with opposing trajectories intersect. Curves are also more likely to cross as FA reaches its asymptotic value during development and individuals converge upon subequal FA. Our simulations do not take this dynamic into consideration, because our assignments of FA to individuals do not consider temporal changes.

Another explanation for the resident effect is that resources such as territories are more valuable to owners than they are to residents because of an information asymmetry (e.g., Parker 1974; Rohwer 1982; Leimar and Enquist 1984; Riechert 1979, 1984; Enquist and Leimar 1987). Ewald's experiments (1985) with hummingbirds are particularly instructive in this regard, although they are described in terms of a resource value asymmetry, reviewed by Enquist and Leimar (1987). Since in many cases successful reproductive opportunities depend upon acquisition of limited and localized resources, it is not obvious why resources should be more valuable to owners than they are to SA-SX nonresidents. The resident effect as expressed in natural populations may be based largely upon patterns of decision-making dependent upon estimates of personal FA, respect for probabilities (Pw), and estimates of the costs of encounters rather than upon asymmetries in absolute resource value.

Under natural conditions, conventional settlements and an apparent resident effect could be inferred from episodic observations in the absence of more continuous observations that clarify the conflict contexts (e.g., van den Berghe 1988). Few naturalistic studies follow individuals closely and long enough to identify outcomes throughout a lifetime and the utility of doing so has not previously been evident.

Dominance hierarchies

Theoretical analyses of linear dominance hierarchies have met with limited success because of the common difficulty of rank quantification. Important questions remain unresolved; e.g., the relationship of individual ability (here FAp) to rank (Landau 1951). How can a high degree of linearity in rank order be maintained (Landau 1965), especially when there are many individuals in the hierarchy (Chase 1984)? Comparison of the FA of individuals in different LDHs has been viewed as an intractable problem because rank is an ordinal value not directly comparable to ranks in other hierarchies. Use of FA percentiles and their associated frequency distributions solves that problem for some purposes by identifying the probability that an individual of a specific rank will attain any other rank in other hierarchies of specified size. In simulations, we make the following assumptions about linear dominance hierarchies:

1. There is an exact ordering of FA among all group members. Individuals with higher FA hold higher ranks.
2. Distribution of FA, as derived above among group members is representative of the FA of all members of the population, including members of other hierarchies.

In our application of the model to linear dominance hierarchies (LDHs) the number of FA values randomly drawn from 0 -100 equals the number of individuals in the hierarchy. Rank ordering of these values identifies individual ranks in LDHs. We thus avoid the problem of dealing with ranked individuals as if they were evenly spaced throughout the LDH, an inappropriate expectation because in hierarchically ordered societies some individuals persistently and sometimes successfully challenge one another while others rarely do so.

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 individuals who are not competitively competent, and they note further that in the case of feeding (or multi-purpose) territories there may be a positive feedback relationship between successful outcomes and future outcomes because the condition of winners is enhanced. The feedback relationship between contest outcomes and growth is especially obvious among fish whose adult size varies widely as a consequence of social dominance, resulting in differences in growth rates (Magnuson 1962; Abbott et al. 1985).

Rank rise by comparison shopping?

An individual might move upward in a hierarchical social system by choosing another LDH where there are weaker individuals (Clutton-Brock and Harvey 1976; Cheney and Seyfarth 1983; Pusey and Packer 1987). But from any perspective, the existence of weaker groups elsewhere is a necessarily transient and unstable condition. It seems unlikely that patterns of emigration have evolved on the basis of improbable opportunities. The potential for upward social mobility in hierarchical societies by choosing residence in other groups needs reconsideration.

We evaluate this possibility by analyzing the probable distribution of individuals by FA in modeled cohorts. The results of this simulation and calculation are given in Figure 5 for cohorts with a specified number of options to enter other cohorts of the same size. Thus, a 5th ranking male in a cohort of 10 males moving into another cohort of 10 males has on the average a 0.016 chance of rising to alpha if he has only one other cohort to choose from and a 0.075 chance of doing so if he can choose among six other same size groups (Figure 5). Choice of another equal size hierarchy will seldom offer more than the gain of one rank if the FA of all cohort members is independent and varies independently, i.e., if there is no social support (S) from other individuals in establishing ranking (McNutt and Hamilton 1989). The same simulation for movement to smaller groups produces the predictable but slight rise in the probability of a rank rise. Only a move to a smaller group or some change in other parameters such as social support and risk taking provide any reliable opportunity for rank rises by changes in group membership.

Figure 5 Here

Conclusion

Fighting ability is a fundamental determinant of the outcome of dyadic interactions. Interpretations of patterns of resource allocation among interacting or competing groups of individuals may benefit from evaluations following from the assumption that all individuals differ in their ability to compete for resources. We described a pattern of frequency distributions of FA as a function of a limited number of costly contests. From our simulations of repeated contests among randomly chosen individuals we show that these patterns exist as a direct consequence of the dependence of contest outcomes upon individual differences in ability. These distributions may provide information to interacting individuals as a function of experience.

We expect animals to respond to these frequencies, which reflect probabilistic information, because of the negative fitness consequences associated with a failure to compete (forfeiture) and to prevail in contests. The probabilities of responding to opponents and the patterns of behavior during responses to them should reflect costs which will differ by species, prior experience, and the value of the contended for resources. As individuals gain experience they may gain a more refined sense of their relative ability. The fitness costs of fighting limit that experience and introduce some error into the degree of correspondence between ability and resource acquisition. Classic studies demonstrate assessment responses may be mediated by hormonal components. If ability is a dynamic lifetime characteristic with a probabilistic pattern of ontogeny (McNutt and Hamilton 1989), an explanation for patterns of behavior resulting in differential access to resources emerges. Explanations for the resident effect in territorial disputes and an interpretation of status gained in linear dominance hierarchies follow.

Table 1. Approximate loser's probability of winning (Pw) against winners.

LOSER RECORD (TIMES)	WINNER RECORD* 0	1	2	3	4
0	1/2	1/3	1/4	1/5	1/6
1	1/3	1/6	1/10	1/15	1/20
2	1/4	1/10	1/20	3/100	.016
3	1/5	1/15	3/100	.016	.007
4	1/6	1/20	.016	.007	1/250

* Records are of wins and losses against the field. Outcomes are determined by relative FA. Pw for winner is 1 - Pw for loser.

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Figure 1. Frequency distribution of fighting ability (FA) in groups with assumptions stated in the text. The total number of contestants is the same in all diagrams but is divided into additional distributions. A, after a single contest. B, after two contests per contestant. The group divided into (1) double winners, (2) double losers and (3) those with a record of one win and one loss. (C) after four contests, (1) with a record of all wins, (2) three wins and a loss, (3) two wins and two losses, (4) one win and three losses and (5) four losses. The distributions in B and C are also the same as for those of ranks of individuals in a linear dominance hierarchy of three (B) and five individuals (C).

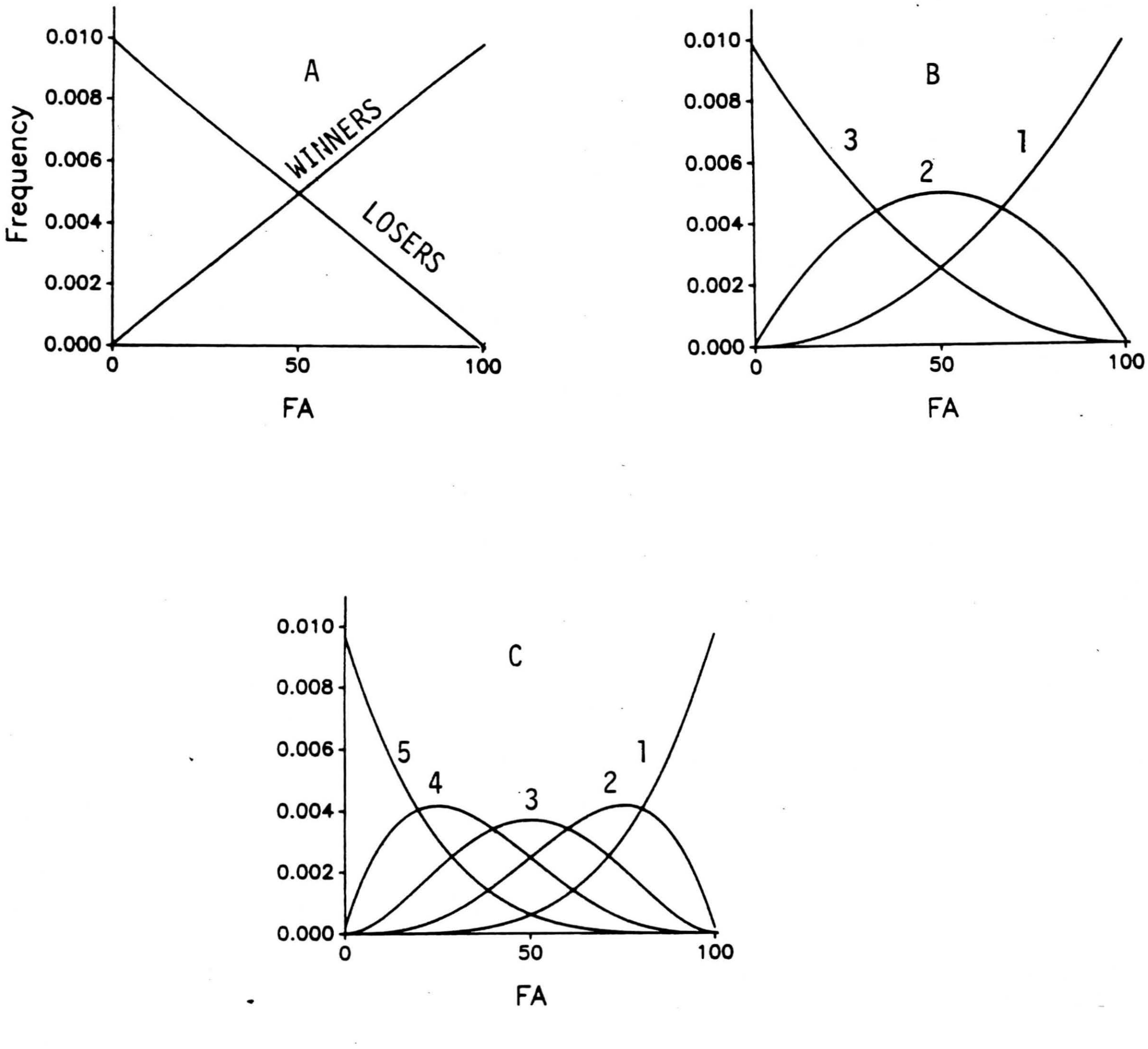

Figure 2. Frequency distribution of individuals by fighting ability (FA). A, individuals with no record, B, with a record of one win and one loss and C, two wins and two losses. The example illustrates the potential for an individual to more accurately estimate its own relative FA based upon contest experience.

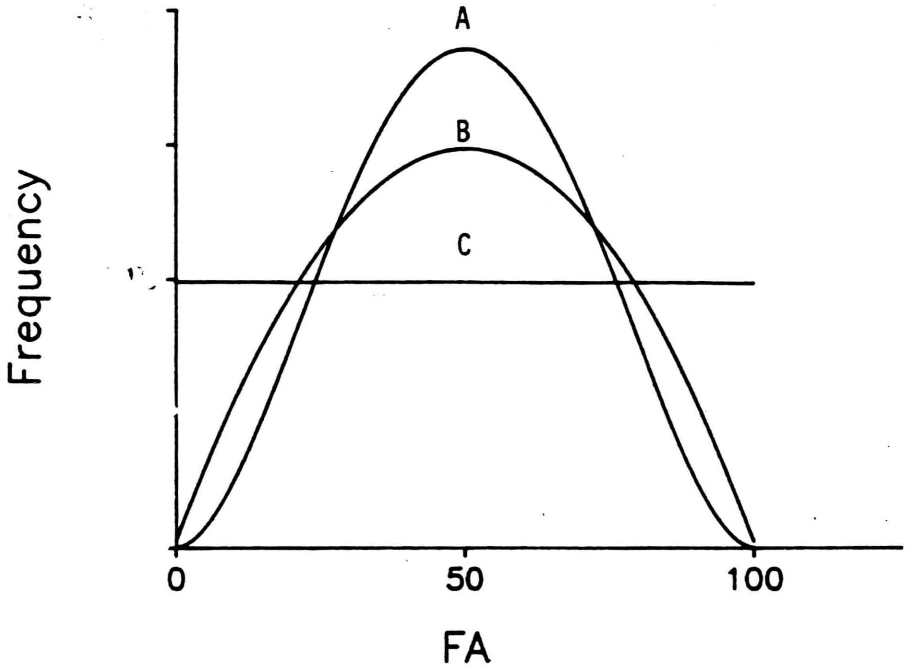

Figure 3. Probability distribution functions of fighting ability (FA) for winners after 1 through 10 rounds of random encounters by losers against winners if 50% of the contestants are excluded from resources. A, for 10 contestants and B, for 100 contestants. The frequency distribution curves are for winners after 1, 2, 5 and 10 contests. Distribution curves of losers are mirror images of those of winners.

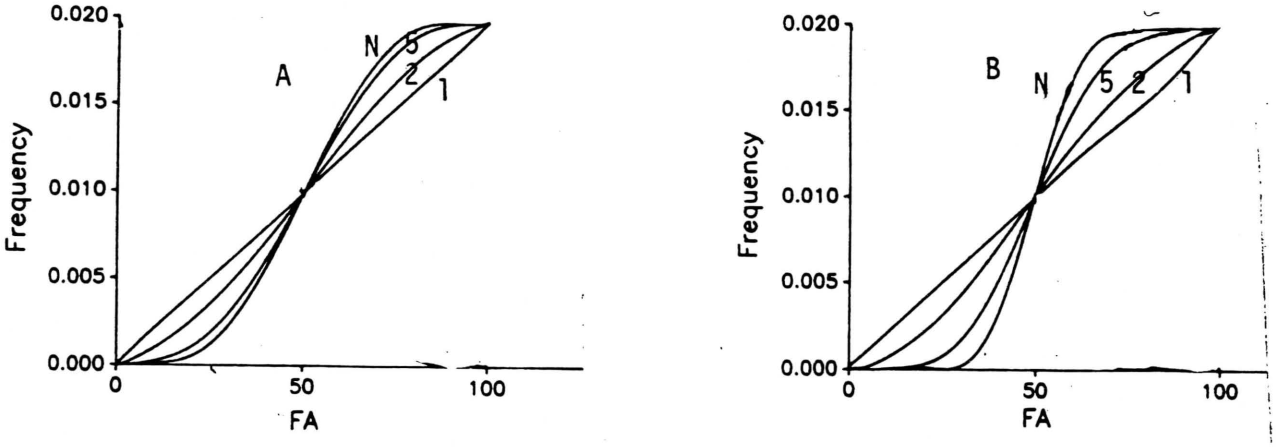

Figure 4. Same as for figure 3, but with proportion of resources or residences adequate to accommodate 70% of the population.

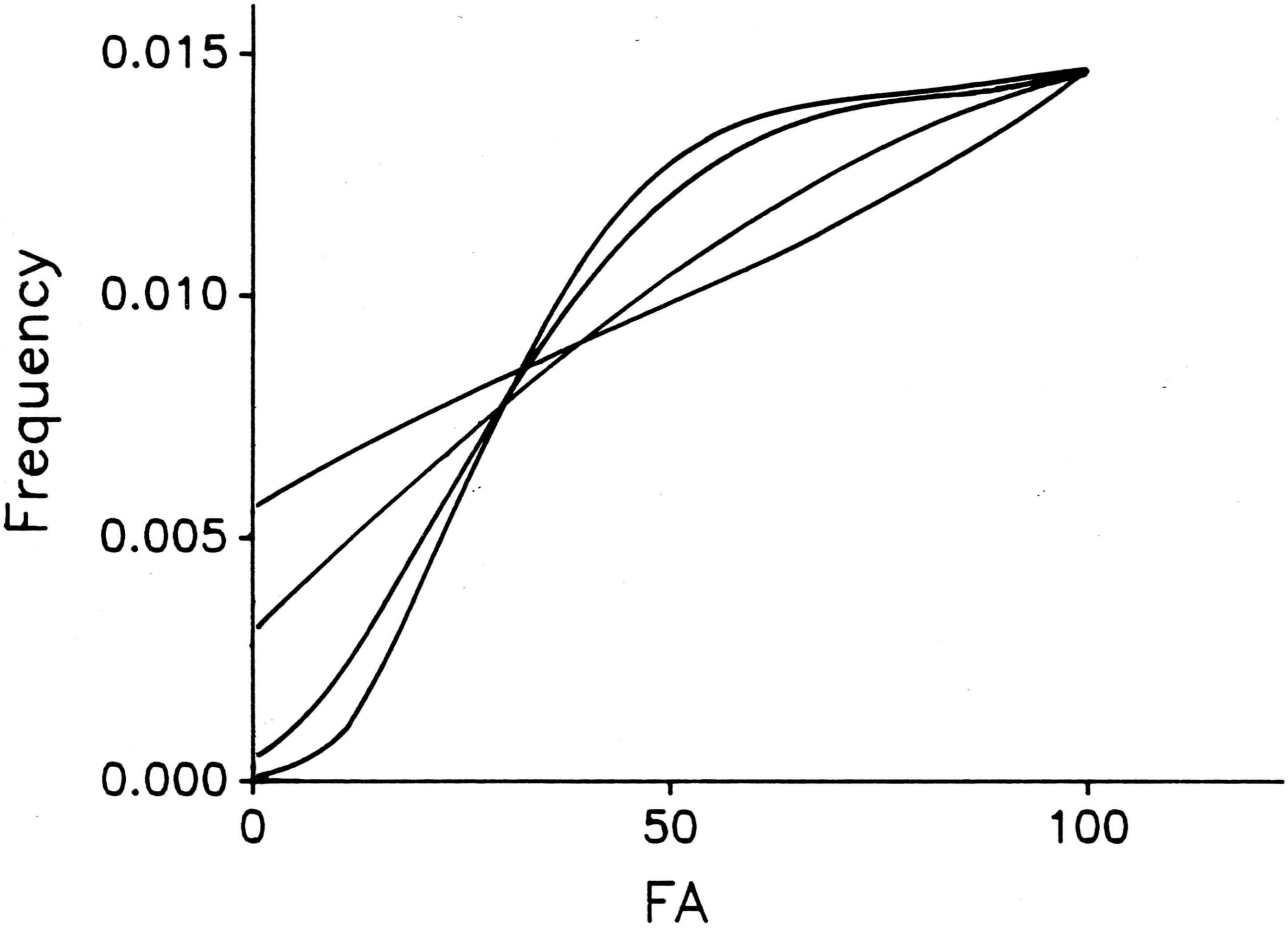

Figure 5. The probability of gaining rank by changing membership to another group based upon fighting ability (FA) in cohorts of 10 individuals. (A), when there is one other group of the same size to test, (B) for two alternatives, (C) for six alternatives, (D) for 18 alternatives and (E), for 36 alternatives.