DOMINANCE HIERARCHY AND SOCIAL ORGANIZATION
STRONG OR WEAK INFERENCE?

I. Introduction

The primate literature has focused attention on dominance hierarchies from the first scientific investigations of primate behavior (Kempf, 1917; Yerkes and Yerkes, 1929; Miller, 1931; Zuckerman, 1932). Interest continued during the pioneering studies of Carpenter (1934, 1935, 1942a, 1942b) however the field studies of baboons by Hall, Washburn, and DeVore (Washburn and DeVore, 1961; Hall and DeVore, 1965; DeVore and Hall, 1965; DeVore, 1965) have made the major impact in recent years. The studies that followed (Rowell, 1966, 1967; Stoltz and Saayman, 1970; Ransom, 1971; Harding, 1973; Hausfater, 1975 and others) yielded contradictory data and the concept of social dominance with its concomitant notion of male hierarchy continues to be controversial not merely in its application to baboon social organization but to that of other primates both wild and captive (Gartlan, 1968; Berstein, 1970; Rowell, 1974; etc.). The research community is divided into two opposed factions, those who believe that dominance hierarchies exist and are of evolutionary importance in primate social organization, and those who don't. Recently Popp and DeVore (in press) re-evaluated the concept of social dominance within a sociobiological framework making specific predictions about hierarchy or the absence of it, perhaps bridging the two positions.

I would like to suggest that the almost obsessive interest in dominance hierarchy may have distorted our perspective and produced a subtle shift in our sense of problem. Further, that

investigations of dominance hierarchy or related behaviors may be representative of our investigations of other social behavior and that these share at least one methodological characteristic, they violate accepted ideas about scientific thinking and scientific method.

"Certain systematic methods of scientific thinking may produce much more rapid progress than others" (Platt, 1964:347). In a paper entitled "Strong Inference" Platt discusses the reasons why some fields of scientific investigation make rapid advances and others do not. He emphasizes the important role played by 1) a sense of problem, 2) the use of inductive inference, 3) coupled with multiple alternative hypotheses, and 4) the critical testing of hypotheses. In scientific proof, as currently formulated (Popper, 1959), hypotheses can only be falsified, they cannot be validated. Yet as Platt points out, as the number of falsified alternative hypotheses increases, inference moves from weak to strong. "(To man) it is granted only to proceed at first by negatives, and at last to end in affirmatives after exclusion has been exhausted" (Francis Bacon as cited in Platt, pg. 350).

The initial "problem" that faced primate researchers was "What was the social organization of the group," and secondly "what was the adaptive significance of this particular type of social organization." Evolutionary significance was couched in terms of group selection but the current trend has favored assessment of individual reproductive success.) Two implicit assumptions have existed: 1) that a social aggregation of primates has a social organization (and it is the investigators' task to find what form it takes, not whether it exists) and 2) that social organization is based on predictability of interactions between individuals. One early solution to the "problem" of the social organization of the group was the concept of male dominance hierarchy. Interpretations of adaptive significance included both male hierarchy as a means for group advantage allowing the most fit males to reproduce, control and protect the group, as well as a means whereby individuals acquire priority of access to resources (incentives) including reproductive females.

With Platt's "strong inference" in mind, I would like to consider baboon dominance hierarchies at two levels. Firstly, how does the concept of male dominance hierarchy fit into a systematic evaluation of social organization. Then I will present the data on dominance hierarchy for a troop of baboons that I observed during 1972-1974.

II. Testing for Dominance Hierarchy: Method

Figure 1 locates male dominance hierarchy in a conceptually useful flow diagram that meets some of the conditions of Platt's strong inference method. For the first step in understanding the basis of social organization (BSO) I have only listed a few hypotheses (k=1-3, leaving the rest to the reader's creativity). At this point we will assume, as have previous investigators, that baboon social organization is based on predictability of social interactions. What then are the possible bases of predictability in a baboon troop? I have

included both ideas found in the literature and ones derived from my own data and imagination.

The basis of predictability (BPred) is divided into two categories: unidimensional (i) and multidimensional (j), although the dimensions included in i are those used in j. The ordering within i is historical; j follows i logically.

i

1. Male dominance hierarchy

   Males in a group organize themselves hierarchically. Hierarchy is normally determined by agonistic interactions. For the males, this agonistically based order is consistent with ordering in other behaviors like grooming, copulation, defense, policing, leadership, etc. The male hierarchy also organizes the group with the behavior of other age-sex classes related to the male system. (This is essentially the DeVore-Hall-Washburn model for baboons.)

2. Female dominance hierarchy

   Females in a group organize themselves hierarchically. While a parallel concept to that of male hierarchy, unlike the male example female hierarchy has never been used as the only explanation of social organization. However, since arguments about male hierarchy do not rely on a comparable female hierarchy, by analogy it is possible to argue for a strictly female determined social organization based on hierarchy.

3. Male-female dominance hierarchy

   Two independent but contiguous hierarchies organize the group. This is a frequent interpretation of data on captive primates.

4. Kinship

   Groupings based on matrilineal descent organize interactions within the group. Dynamics of interaction are different within kin groups and between kin groups. Evidence comes from longitudinal studies on primates.

5. Age

   When different age cohorts exhibit different behaviors, a chronologically stratified group results. This idea is implicit in studies of ontogenetic development and in age-sex class treatments of social behavior. Rowell (1972) has pointed to the possibility of age structuring among adult individuals.

6. Affiliation

Affiliation occurs between biologically related individuals but also between unrelated individuals. Here it refers to the latter, although I suggest that it acts in a manner similar to that described for kinship.

j

1. Multidimensional hierarchically effective

Two or more of the dimensions listed under "i" are effective but in a hierarchical order. Predictability begins with i = n but when this doesn't differentiate response it goes to i = n+1, etc. in each interaction. In "j" as a principle of operation of dimensions, "i" could be 1 through 6 or any subset thereof and hierarchically ordered in many ways.

2. Multidimensional context specific

Two or more of the dimensions listed under "i" are effective but their operation is context specific.

These are possible alternative hypotheses for the basis of predictability of interactions that underlies social organization. Seen within this conceptual scheme, male dominance hierarchy is only one such hypothesis. Ideally alternative hypotheses should be mutually exclusive and tests of hypotheses should involve critical experiments that exclude the greatest number. For behavioral field data, critical experiments that test hypotheses are difficult and rare. There are exceptions such as Kummer's work (1971a, 1971b). However, natural experiments, where important variables are manipulated, do occur. Furthermore, comparison of data between groups, populations, and habitats as well as longitudinal data on the same group may at times fulfill some of the requirements of testing.

Beginning with a data file of behavioral interactions, analysis of predictability involves two steps. In the first step, one social behavior (or behavioral category) is analyzed for directionality of interactions and consistency or stability of outcomes. We might call this "level 1" predictability. Then other social behaviors are analyzed to see whether there is the same directionality and consistency as found in the first analysis. This continues until all behaviors (as divided into categories by investigators based on evolutionary function or some heuristic criteria) have been treated. The predictability found at this point can be termed "level 2" and might be synonomous with social organization. For example, agonistic interactions between adult male baboons are analyzed and directionality of interactions and consistency of outcomes are noted. A male dominance hierarchy is constructed. Then grooming, copulation, mounting, presenting, etc. are analyzed in the same manner and related back to the male hierarchy constructed from the first analysis. However, in this example, level 1 analysis focused on only one age-sex class, the males. Therefore analysis of level 2 predictability must also include the behavior of other age-sex classes, the directionality of interactions, the consistency of outcomes, and the relationship of these to the male dominance hierarchy.

Usually investigations of primate social organization have implicit this type of scheme. A frequent scenario is as follows: the investigator, assuming social organization and predictability of interactions, arrives at the first hypothesis (i = 1, male dominance hierarchy) tests for level 1 predictability (for males only) then tests for level 2 predictability (for males only) finds a positive result for males in both (infers rather than systematically tests predictability for other age-sex classes and its relationship to male hierarchy) then moves on to the second problem, that of interpreting the adaptive significance of this type of social organization. Here the process stops. The difficulty begins when others, reaching i = 1 do not have positive results. Historically, in the controversy that followed, neither faction went on to systemically test alternative hypotheses although the anti-dominance contingent did make useful suggestions about other social organizing principles (bases of predictability).

Since it is not possible to prove a positive result, the difficulty with this method is apparent. Testing only for male dominance hierarchy and finding it results in weak inference. Only by excluding other, alternative, hypotheses (i = 2-6, j = 1-2) does acceptance of male dominance hierarchy as the basis of predictability of interactions in a group move to strong inference.[1]

When the data are observational and not experimental this problem with method is especially critical. It is also important when the fit between data (outcome of agonistic interactions)

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[1]For example, male dominance hierarchy may be obtainable from the data but what if similar results (directionality and stability) can be extracted using another dimension or more than one. Without testing other hypotheses how do we determine what is really operative? Can we assume it is the dimension we tested first?

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and organizing principle (dominance status) is not perfect, a frequent situation in analyses of male dominance hierarchies. Reversals, irregularities, inconsistencies might be clues to the operations of other variables implying that alternative hypotheses should be considered.

III. Testing for Dominance Hierarchy: Baboon Data

A. Study Population

I conducted a field study of one troop of olive baboons (*Papio anubis*) from September, 1972 until January, 1974 on Kekopey Ranch near the village of Gilgil in the Central Rift Valley of Kenya. The habitat is high altitude savannah with rainfall averaging 670mm and temperatures between 8 and 27 degrees centigrade (Blankenship and Qvortrup, 1974). The ranch covers 450 hectares that has been altered for cattle raising during the last 20 years by bush clearing and construction of a system of cattle troughs bringing water into areas previously without it. The maximum carrying capacity of the ranch is 3,500 head of cattle although as few as 300 head were present during the study period. Of the central 180 hectares within which the troop's 19.8 km^2 home range (Harding, 1973) is found, 52% is grassland of which 40% is pre-existing and 12% is the result of bush removal. The remainder is bush of various types with leleshwa (*Tarchonantus camphoratus*) predominating. Large carnivores have been shot or trapped since the early 1900's however a healthy leopard population still remains along with three species of jackals, bat-eared foxes, and feral domestic dogs that hunt in packs. Occasional hyena, lion, and cheetah also prey on the cattle.

A large biomass of other wildlife coexist with the cattle. Baboon and ungulate populations have increased rapidly as a result of ecological modification (Blankenship and Qvortrup, 1974). In 1970, seven baboon troops were located in the central area with group sizes from 35 to 125 (Harding, 1973); population density was estimated at 10.3 baboons/km^2. This is a high density figure for savannah baboons. By 1977 the same area contained roughly 19 baboons/km^2 (Strum, personal observation).

While few humans actually reside on the ranch, local inhabitants account for much of the cattle and wildlife mortality.

Observation of the focal troop (PHG) began in 1970 with R.S.O. Harding followed by W. Malmi in 1971. By 1972 the troop had become habituated to observation from a white Volkswagen bus and identification of all adult males and some adult females and infants was completed.

In December, 1972 I began habituation of the baboons to observation on foot and identified the remaining troop members. In 1973 the troop averaged 7 adult males, 19 adult females, 24 juveniles, 13 infants.[1] During 1,200 hours of direct observation on PHG I employed several techniques of data collection following Altmann (1974). I sampled all individuals 4 years of age or older as focal subjects for 15-minute periods

[1]Age classes follow Rowell (1967) and Ransom (1971) however males are classified as adult at 8 years and older rather than 6 years of age and as subadults from 5 to 8 years rather than 4-6 years.

according to a predetermined schedule. Additional <u>ad lib</u> sampling focused on social interactions falling into the broad categories of approach, avoidance, aggression, sexual behavior, and affiliation (grooming, greeting, etc.). Special attention was paid to polyadic social interactions. <u>Ad lib</u> data on intertroop encounters and predatory behavior were also recorded. Daily records were kept of copulations, consorts, sexual state of all females, injuries, and demographic changes.

B. <u>Procedure: Male Dominance Hierarchy</u>

In my analysis of the data I have assumed, as have others, that a social aggregation of baboons has a social organization and that the basis of this social organization is predictability of interactions between individuals. I then asked "what is the basis of this predictability?" and tested for an agonistically based male dominance hierarchy (i = 1).

<u>Dyadic Analysis</u>

Stevens (Sokal and Rohlf, 1969:628) has considered the phenomenon of sequences of same sign alternatives within a probabilistic framework. Where two alternatives exist, a test of divergence from chance ordering in a time sequence has been developed from Stevens earlier work. This test of temporal trends "t" utilizes a normal approximation to the data since the distribution of alternatives in sequence will be normally distributed if allowed to occur by chance.

A consistent and predictable dominance hierarchy should have several characteristics when analyzed in this fashion. It should reveal relatively few changes in polarity during the sequence of interactions between two individuals and changes, if they occur, should be either of very short duration (when dominance relationships are stable) or of very long duration (when the relationship between the interactants has been reversed). If a consistent principle of interaction is operating, a stochastic model of interactions should have a poor fit with the data on agonism. In that case, the normal approximation to the "runs" (temporally adjacent behavioral outcomes having the same individual scored as the "winner") retrieved from the behavioral data should reveal a confidence interval significantly greater than that expected if the interactions were resolved on the basis of chance variables.

Data from 167.25 hours of 15-minute focal animal samples on 10 males (from March, 1973 to January, 1974) were encoded onto computer cards and stored on tape for selective retrieval. Agonistic behaviors similar to those used by other investigators in determining dominance hierarchies were chosen for retrieval for each interacting subject dyad (see Table 1). Only dyads for which there were ten or more bouts of agonistic behavior are included in this analysis. An agonistic bout was defined as a sequence of behaviors that included any of the behaviors listed in Table 1. This sequence might be lengthy but as long as the agonistic behaviors were continuous and contiguous, only one bout was scored. A bout was considered terminated when the actors no longer directed agonistic behaviors towards each other.

The result of the analysis is a 2 by n matrix for each dyad where n is the total number of bouts. Bouts were sorted into chronological order and each bout scored. Since an interaction involves two individuals, the animal being sampled (the focal animal) and an interactant, every bout was scored as a "win" (1) or "loss" (0) depending upon the outcome of the bout from the point of view of the focal animal. Procedure and criteria for determining winners or losers followed Hausfater (1975):

> A winner and a loser were determined in an agonistic bout only when one animal directed one or more submissive behaviors, and no aggressive behaviors, toward a second animal in response to aggressive behaviors (or any other set of nonsubmissive behaviors) from the second animal. The individual who gave the submissive behaviors was considered the loser of the bout, and the individual who gave only aggressive and/or other nonsubmissive behaviors was considered the winner of the bout.

The "t" distribution was used to calculate confidence intervals for the temporal sequences of outcomes of these dyadic agonistic bouts.

Three of the ten resident males were eliminated from this analysis because of their short tenure in the troop during focal sampling (less than 1 month).[1] Of the 21 dyads, 16 had 10 or more agonistic bouts (n = 316) as recorded during focal animal sampling. Of these 16, 11 dyads did not diverge from a chance distribution, where t_s greater than 3.29 occurs by chance with a probability of .001, while 5 showed a significant divergence (p = .001). The mean value of t_s for males was 2.78

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[1]The remaining seven males had a total of 156.5 hours of focal samples.

with a standard deviation of 1.47. Given these results, it is not possible to reject the hypothesis that the pattern of interactions associated with agonism is random with respect to identity of actor and outcome, for males as a class.

Since focal samples were supplemented by ad lib data on male agonism, these data were analyzed next. The total 195 ad lib agonistic bouts did not provide sufficient bouts per dyad to allow a test of temporal trends. However, by integrating these data into their proper temporal sequence in the focal sample data a second "runs" analysis was possible. In the second analysis 4 of the 5 previously untested dyads could be considered. In total, 20 of 21 dyads were analyzed using the combined focal and ad lib data. The 4 new dyads did not diverge from a distribution expected by chance while 3 of the previous 5 "nonrandom" dyads now showed a random pattern in the combined data. The remaining 11 dyads retained their previous pattern of randomness.

In the combined data, 18 rather than 11 dyads showed a distribution of interactions that could not be distinguished from chance while 2 revealed "nonrandom" patterns. The new mean value of t_s for males was 2.30 as compared to the previous mean value of 2.78.

Nonrandom distribution of outcomes can emerge in this type of analysis in several ways. For one dyad, the observed pattern was frequent and temporally equivalent reversals (111 agonistic bouts with 38 runs from the focal data, 142 bouts with 51 runs from the combined data). Here the divergence from chance is

a consequence of the regular and constant trading back and forth between the two dyad members. But this does not meet the expectations for outcomes that result from dominance hierarchy despite the nonrandom quality of the interactions. The other dyad was similar in pattern but with fewer bouts and more time between reversals.

Consideration of the total number of agonistic bouts yields results not in conflict with the data previously presented. There were 531 agonistic bouts between 7 males when both focal samples and ad lib data are combined. Of these, 326 were reversals of outcome from the previous interaction for that dyad.

It is clear from the above analyses that most male dyadic agonism has outcomes that cannot be predicted from a knowledge of the outcomes of previous episodes. It is therefore not possible to construct an agonistically based male dominance hierarchy from the data on dyadic interactions.

Polyadic Analysis

Male agonism may become polyadic, involving more individuals than just the initial interacting pair but exhibiting the same agonistic behaviors as listed in Table 1. Many kinds of polyadic agonistic interactions are possible; the ones considered here result when additional males join a dyadic encounter after it has reached the level of medium intensity aggressive threat. The total number of interactants may range from three to six males.

There were 100 polyadic agonistic bouts of this particular kind in the focal sample data (compared to 336 dyadic bouts) while there were 152 polyadic ad lib bouts (compared to 195 dyadic bouts). The disparity in proportion between data files probably reflects the differential sensitivity of the two sampling methods.

The ad lib data on polyadic agonism were analyzed to see if a predictable pattern of interaction between males could be discerned. Bouts were defined and scored as for dyadic interactions and special attention was paid to outcome vis-à-vis the initial interactants. Temporal trends analysis was not used as the total number of bouts was less than 10 for any dyad.

Scoring outcomes of polyadic encounters was more difficult as the number of participants increased, for as these increased, so did the undecidedness of the bout (undecided bouts are ones for which a winner(s) or loser(s) cannot be determined). A linear regression line best fitting the points is $y = .26x - .33$, where the y coordinate is the number of actors and the x coordinate is the proportion of undecided bouts. The coefficient of determination (r^2) is larger than .99, thus the number of actors "explains" almost entirely the proportion of undecided bouts. By contrast, less than 1% of all male dyadic agonistic bouts were undecided.

In decided polyadic bouts (n = 90), the outcomes in 57% of the cases were consistent with the previous dyadic interaction between the initial pair of actors while 43% of the cases showed reversal of outcomes. In 14% of all the decided bouts both an initial actor and a joining male showed reversals in outcome from previous interactions. For undecided bouts, if we allow

ourselves to make predictions about outcomes based on the previous agonistic bout for pairs of males, then the outcome consistent with the preceding interaction would have been a win for the aggressor in 65% of the cases while it would have been a loss for him in 35% of the cases.

The proportion of undecided polyadic agonistic bouts and the frequency of reversals in decided bouts, precludes the use of polyadic interactions in the place of dyadic interactions for construction of an agonistically based male dominance hierarchy. However a type of predictability of interaction that lends itself to further interpretation does emerge from the analysis of polyadic bouts (Strum, 1978).

Contextual Analysis

In the previous analyses, agonistic interactions were combined regardless of context. Yet separating agonistic bouts by context (resource related?) might reveal a consistency in outcomes that is otherwise obscured. Ad lib data on dyadic and polyadic interactions were analyzed in this manner as there was better contextual information for them than for focal sample data.

Aggression was divided into contexts when it occurred around and could be related to:

1. estrus female
2. unaffiliated and nonreceptive female
3. affiliated and nonreceptive female
4. meat consumption
5. foods other than meat
6. intertroop encounter
7. migrating male
8. ongoing male aggression apparently unrelated to a resource (polyadic only)
9. greeting behavior
10. undetermined

Temporal trends analysis could not be employed as too few dyads had 10 or more bouts per dyad per context. While the data are limited and the number of interactions per dyad per context few, no new stability or consistency emerges that would allow the construction of an agonistically based, context-specific series of dominance hierarchies.

Conclusions

No additional tests of the hypothesis that the basis of predictability of interactions is a male dominance hierarchy (i = 1) are possible with the data collected during my 1972-1974 study on PHG baboons. From the present analyses several conclusions can be reached.

1. Most male-male agonistic encounters have outcomes that cannot be predicted from a knowledge of the outcomes of previous episodes.
2. The pattern of agonistic interactions cannot be statistically discriminated as different from that expected if outcomes were determined by a chance variable for most male dyads and for males as a class.
3. Dyadic relationships are not consistent over time for any but a small number of dyads.
4. An agonistically based dominance hierarchy for males cannot be constructed using either dyadic or polyadic interactions whether context-free or context-specific.

I would like to suggest that for PHG baboons in 1973 it is possible to reject the first hypothesis in our search for the basis of predictability of interactions underlying social organization. I have the following qualifications. I do not consider the analysis of context-specific agonistic interactions to constitute a satisfactory test of that concept. Further data should be collected to eliminate the possibility of multiple context-specific dominance hierarchies among the males.

Another possibility that has not been treated is the existence of conditional strategies as conceived of by game theorists and applied to animal conflicts (Maynard-Smith and Price, 1973; Parker, 1974; Maynard-Smith, 1976). However, while either context-specific hierarchies or conditional strategies may provide a means whereby interactions between males can be analyzed to produce consistency of outcomes in agonism (at level 1 predictability) neither would represent what is traditionally conceived of as a male dominance hierarchy and so the concept would have to be re-evaluated. Furthermore, because of the nature of these strategies of interaction, I would expect tests of level 2 predictability to yield negative results.

C. Female Dominance Hierarchy

Dyadic Analysis: Female-female interactions

Having rejected hypothesis i = 1, male dominance hierarchy, I next turned to hypothesis i = 2, female dominance hierarchy. During the same field study 20 adult females were sampled as focal animals from January, 1973 until January, 1974 for 473 hours (1,892 samples). One female disappeared after 16 samples were completed; she has been omitted from this analysis.

Focal sample data on adult females were analyzed in an identical manner to that on adult males. There were 171 possible female dyads and 97 of these had ten or more agonistic bouts (n = 1975). Of these 97, only 7 dyads had patterns of outcomes of agonistic interactions that were not distinguishable from a chance distribution, where t_s greater than 3.29 occurs by chance with a probability of .001. However, the high values of t_s for the other 90 female dyads were the consequence of a different arrangement of interactions than that producing high t_s values for the two male dyads previously considered. A relatively high rate of reversals giving consistent outcomes over short periods of time was responsible for the high male t_s values. By contrast the high scores for female dyads resulted from a small number of reversals and a consistency of behavior over long periods of time (i.e. "relatively few changes in polarity during the sequence of interactions between two individuals and changes... of very short duration"). The female pattern conforms to expectations about how bouts would be ordered by the operation of a dominance hierarchy while the male pattern does not.

The number of runs expressed as a ratio of the total number of interactions can be used as a measure of stability in interactions between dyad members over time. For females the mean ratio of runs to bouts (r/n) is .22 (S.D. = .14) and for males the mean ratio is .38 (S.D. = .14). As the sample size is large and means of samples drawn from a normal distribution are themselves normally distributed a t test of means was used to compare the mean r/n ratios. This test is robust (the variances of the male and female ratios are equal) and generates a t value of 4.43 with 94 degrees of freedom. Thus the difference between males and females is significant with a confidence interval much greater than .001. We can conclude that female dyads have more stability in interactions over time than male dyads.

The remaining 428 interactions from female focal samples averaged 5 agonistic bouts per dyad for the female dyads not yet considered (n = 74). Although it was not possible to test for temporal trends in outcomes for these data, it was the case that no reversals of outcome occurred in 49 dyads, one reversal of outcome occurred in 2 dyads, and two reversals of outcome occurred in 23 dyads (changing the "relationship" back to its original directionality of outcomes). Reversals were primarily confined to one sample day per dyad. In total 253 reversals took place in 2,405 agonistic bouts from all focal samples on females.

Using only focal sample data a tentative hierarchy can be constructed for females. Initially the data from the 90 dyads containing 10 or more agonistic bouts of nonrandom outcome were used. Next, dyads with fewer than 10 bouts but no reversals in outcome were placed within this system. Finally, the 7 "random" dyads were checked against the existing order. Linearity was clear-cut in this hierarchy in all but two positions. Three females showed the following characteristics in rank 11: DB over M, M over F (from among the initial 90 dyads) but DB equal to F (from 6 focal bouts). Analysis of additional ad lib data (n = 8) indicated an equality between females DB and F. Other PHG females consistently ranked above or below all three of these females. Another equality between two females occurred in the last rank (4 focal bouts). There were no ad lib data on agonistic interactions between this pair.

A sampling of ad lib data on female agonism (n = 423) does not indicate any conflict with the hierarchical ranking determined from the focal sample data.[1]

Dyadic Analysis: Other interactions

If we accept that these data represent an adequate and sufficient test of level 1 predictability for an agonistically based female dominance hierarchy then tests of level 2 predictability must follow. Analysis of other types of social interactions between females and their correlation with female rank is in progress. However, even a positive result for all categories will satisfy only part of the requirements of level 2 predictability of interactions between members of other age-sex

[1]Within this hierarchy, the hypothesis that the instability within dyads for the 7 "random" dyads is related to closeness of rank cannot be rejected in only 1 case. Furthermore reversals within these dyads occurred in relationship to the birth of a new infant to one of the females in only 1 of the 7 cases.

classes is an important part of hypothesis i = 2.

To this end, agonistic interactions between adult females and immatures (age 2 to 5) and between immatures themselves were considered. Only individuals 4 years or older were sampled as focal subjects therefore most of the data for these analyses comes from focal samples on adult females with additional samples on two females approximately 4 years of age (n = 26) and 3 males of approximately 4-5 years of age (n = 56). The total number of agonistic bouts from these focal samples was 1,119. Nineteen dyads had 10 or more agonistic bouts (n = 312) and these were treated as above.

The mean value of t_s for 10 dyads involving the two adolescent females and adult females was 4.79 (S.D. = 2.29) with a mean r/n ratio of .22 (S.D. = .13).[1] The outcome of agonism between adolescent and adult females fits the adult female pattern. Using data from all focal interactions, the two adolescent females could be placed within the adult female hierarchy at a rank just below their putative mothers. These rankings were tested against a sample of ad lib interactions (n = 97) and found to be consistent.

The mean value of t_s for 7 dyads involving immature males age 4-5 and adult females was 4.10 (S.D. = 1.94) with a mean r/n ratio of .21 (S.D. = .20). These immature males won in agonism with adult females including females who ranked higher than their putative mothers. The pattern of outcomes more more closely resembled the adult female model in terms of non-

[1]Adult female mean t_s was 4.59 and mean r/n was .22.

randomness and stability than the adult male model.[1]

The remaining 807 focal sample bouts were examined to see whether immatures rank as their mothers do in interactions with adult females. This seems to be the case for dyads (n = 197) for which there are data with the exception of immature males 4 years of age or older. There are hints in these data that as immature males begin their growth spurt they change their position vis-à-vis adult females until they rank over all females (I completed 1,200 hours of observation on adolescent males during 1976-1977, in preparation). Mothers (putative and known kinship) ranked over sons until the beginning of the male growth period; mothers ranked over immature daughters including the two cases of putative mother-adolescent daughter pairs.

Rank between adolescent males and adolescent females was less consistent (mean t_s = 2.72; mean r/n = .33) but more data are required before definitive statements can be made (L. Scott completed a study on adolescent females during 1976-1977).

Ad lib data (n = 378) suggest that ranking among immatures is tied to maternal rank with the exception of males age 4-5 years who rank themselves according to other factors (size, strength, "personality"?).

Agonistic interactions between adult males and adolescent males from focal samples (n = 32) displayed a mean t_s of 3.88 with a mean r/n ratio of .23 for 3 dyads. From these data

[1]Adult male mean t_s was 2.78 and mean r/n was .38.

agonism between adult and adolescent males seems to resemble the female model of nonrandom outcomes and relative stability; adolescents generally lost to adult males. Other focal sample data (n = 108) showed no reversals in 10 adolescent-adult male dyads, 1 reversal in 6 dyads, and two reversals in one dyad, supporting this suggestion.

Conclusions

The data collected for PHG baboons in 1973 indicate the presence of an agonistically based female dominance hierarchy that does not permit hypothesis i = 2 to be rejected at level 1 predictability. Furthermore, the female dominance hierarchy can be used as the basis of predicting outcomes of agonistic encounters between immatures and adult females with the exception of males over the age of 4. Maternal rank probably predicts outcome of agonism between immatures including males within age cohorts up to 4 years of age. However, interactions between adolescent males and adolescent females may be less consistent.

Adequate testing of level 2 predictability of female dominance hierarchy requires both the analysis of other interactions between females and their correlation with female rank, and analysis of all categories of interaction between other age-sex classes and the relationship of these to the female dominance hierarchy.

D. Conclusions from the Data

Only tentative conclusions can be made about the basis of predictability of interactions in this troop of baboons.

There is no agonistically based male dominance hierarchy and we can therefore reject i = 1. There does seem to be an almost linear agonistically based female dominance hierarchy (we cannot reject i = 2 at level 1 predictability). This female hierarchy is at least a partial basis of level 2 predictability as demonstrated in some of the agonistic interactions of immatures. However, the female hierarchy is not the basis of outcomes of agonism for any male over 4 years of age (including adult males). It is clear, even without additional data analysis, that female hierarchy cannot be the sole basis of predictability of interactions thus allowing us to reject hypothesis i = 2. Hypothesis i = 3 (male-female dominance hierarchy) can also be rejected despite the existence of a female hierarchy because a male hierarchy is lacking.

Hypothesis i = 4, 5, 6 and j = 1, 2 remain to be considered.[1]

IV. Finale

I hope that my treatment of information on PHG baboons has hinted at the usefulness of "strong inference" for behavioral data. In the case of the controversy about dominance hierarchy, this method refocuses attention on the real "problem" as initially formulated (the basis for predictability of interactions underlying social organization). Male dominance hierarchy (i = 1) or any other single hypothesis

[1]Interesting questions about baboon behavior pose themselves as a result of the preceding analysis. They will be considered elsewhere.

about interaction (i = 2-6, j = 1-2, etc.) is of interest primarily as it bears upon the more comprehensive issues (BSO or BPred) and itself can only be considered a subsidiary "problem." The important issues will not be resolved at this point in the dominance controversy by additional studies of dominance hierarchy but by more extensive testing of alternative hypotheses for the data already generating the controversy.

Formal and systematic application of the method of inductive inference would have immediate benefits for problems in the area of primate behavioral research. Foremost, the method highlights the necessary steps of analysis.

> On any new problem, of course, inductive inference is not as simple and certain as deduction, because it involves reaching out into the unknown. Steps 1 and 2 (devising alternative hypotheses; devising a crucial experiment) require intellectual inventions, which must be cleverly chosen so that hypothesis, experiment, outcome, and exclusion will be related in a rigorous syllogism... What the formal scheme reminds us to do is to try and make these inventions, to take the next step, to proceed to the next fork, without dawdling or getting tied up in irrelevancies. It is clear why this makes for rapid and powerful progress. For exploring the unknown, there is no faster method; this is the minimum sequence of steps. Any conclusion that is not an exclusion is insecure and must be rechecked. (Platt, 1964:347).

In addition, formalization of the problem exposes implicit assumptions and presents us with a logical tree related to the problem. We can precisely pinpoint where we have chosen to begin and if results are ambiguous it may be that previous assumptions require new consideration--a step backwards in the process before we can hope to take another step forward.[1]

[1]This seems particularly germaine to discussions of social organization. The data on agonistic interactions among PHG

male baboons may call into question assumptions about predictability of social interactions (Hamilton's (1971), "selfish herd" challenges existing ideas about the relationship of social aggregation to social organization). Rather than accepting k = 1 in our flow diagram (Figure 1) it may be necessary to actually test alternative hypotheses before proceeding on to tests of derived hypotheses.

There might also be another benefit. Since each scientist is required by this method, to devise and test alternative hypotheses himself, traditional in-fighting, where competing hypotheses have different owners, loses ground. Within the framework of multiple hypotheses, researchers cannot maintain strong emotional investment in any particular one. Competition becomes who can complete the process creatively and quickly rather than who can be most persuasive in convincing others of one's own idea or successful in disproving the "pet" idea of another investigator.[1]

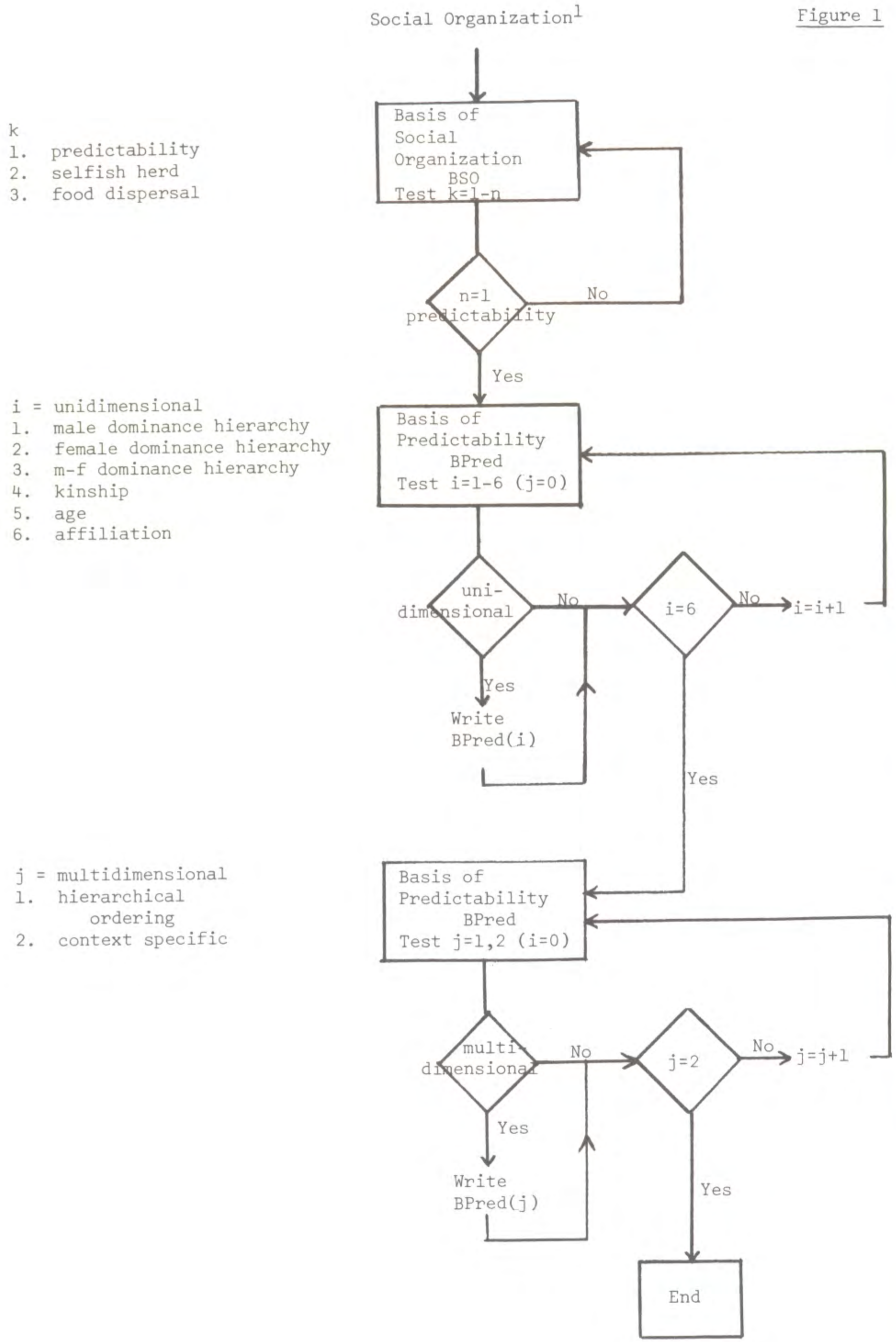
While success in fields that use the strong inference method like molecular biology and high energy physics should be reassuring, I can see objections raised to its application in problems involving "behavior" particularly naturalistic behavior where critical experiments are not so readily available. Yet for a start, with creativity and ingenuity, (and cooperation between investigators in supplying the necessary data) satisfactory critical tests of hypotheses can be constructed employing comparisons of data whether for one group over time

[1]A common scientific practice today is to try and falsify the hypothesis of a competitor while shading one's own hypothesis from scrutiny.

or for different groups, or populations.[1]

[1]I would like to thank R. H. Byles for assistance with statistical analysis and computer processing and R. D'Andrade, E. Hutchins and G. Peterson for assistance with computer processing.

Figure 1



[1]This diagram illustrates a formalized and systematic way of addressing issues in behavior at various levels (i.e. kinship or dominance substituted for "social organization).

TABLE 1
AGONISTIC BEHAVIORS

Aggressive Behavior	Description
A. Low intensity aggression	
1. directed stare	obvious
2. raised eyebrows	sometimes accompanied by lowered eyelids
3. ears flattened	ears pressed against head
4. head bob	jerking head down and forward
5. yawn	mouth opened exposing canines to varying degrees depending on intensity--oriented towards another individual
6. molar grind	jaws rotated with lateral emphasis; audible grinding noise
7. ground slap	palm of hand slapped against ground or substrate
8. broken grunting	low volume rapid series of grunts with orientation towards another individual
9. pant grunt	loud two-phased grunt directed towards another individual
B. Medium intensity aggression:	some combination of elements in #A
C. High intensity aggression:	
1. lunge	short but rapid forward movement towards another individual
2. chase	obvious
3. charging run	an attack
4. aggressive contact	grab, hit, push, grapple, slamming to ground, pressing to ground, standing on, bite

Submissive Behavior	
1. avoid a stare	glancing away from another individual or fixation on the ground
2. fear face	grin or grimace
3. cough geck	single sharp sound with cough-like quality often accompanied by jerks or body twitches
4. tail up	tail is raised and held in a vertical position
5. scream	high pitched relatively continuous sound
6. active avoid	direct movement away from another individual; orientation is obvious but no vocal or gestural communication accompanies movement
7. active avoid: moderately fearful	avoid with rapid movement and repeated glances or fear face or geck or tail up
8. active avoid: fearful	running away with combination of geck, scream, fear face and tail up
9. crouch	body lowered to the ground--orientation to another individual
10. hide	avoid contact by hiding out of sight--adult males frequently use pig-holes
11. approach: moderately fearful	oriented approach with tail up or fear face or geck
12. approach: fearful	oriented approach with tail up and fear face, geck or scream
13. counter-attack	counter chase with submissive elements

Bibliography

Altmann, J.
1974 Observational study of behavior: sampling methods. Behaviour, 49:227-267.

Berstein, I.
1970 Primate status hierarchies. In Primate Behavior, L. Rosenblum ed., New York: Academic Press.

Blankenship, L. and S. Qvortrup
1974 Resource Management on a Kenya ranch. Annual South African Wildlife Management Association, 4:185-190.

Byles, R. and S. Strum
m.s. Natural selection and reproduction among female olive baboons. (submitted to Science).

Carpenter, C. R.
1934 A field study of the behavior and social relations of the howling monkeys. Comparative Psychology Monographs, Vol. 10(2).

1935 Behavior of red spider monkeys in Panama. Journal of Mammalogy, 16:171-180.

1942a Sexual behavior of free-ranging rhesus monkeys. Journal of Comparative Psychology, 33:142-162.

1942b Societies of monkeys and apes. Biology Symposium, 8:177-204.

DeVore, I.
1965 Male dominance and mating behavior in baboons. In Sex and Behavior. F. Beach ed., New York: John Wiley and Sons.

DeVore, I. and K. Hall
1965 Baboon ecology. In Primate Behavior. I. DeVore ed., New York: Holt, Rinehart and Winston.

Gartlan, J.
1968 Structure and function in primate society. Folia primatologica, 8:89-120.

Hall, K. and I. DeVore
1965 Baboon social behavior, In Primate Behavior. S. DeVore ed., New York: Holt, Rinehart and Winston.

Hamilton, W.
1971 Geometry for the selfish herd. Journal of Theoretical Biology 31.

Harding, R. S. O.
1973 Range utilization by a troop of olive baboons. Unpublished dissertation. Berkeley: University of California.

Hausfater, G.
1975 Dominance and reproduction in baboons. Contributions to Primatology. Volume 7. Basel: S. Karger

Kempf, E. J.
1917 The social and sexual behavior of infrahuman primates with some comparable facts in human behavior. Psychoanalytic Review IV:127-154.

Kummer, H.
1971a Immediate causes of primate social structures. In Proceedings, 3rd International Congress Primatology Vol. 3:1-11. H. Kummer ed., Basel: Karger.

1971b Primate Societies. Chicago: Aldine.

Maynard-Smith, J.
1976 Evolution and the theory of games. American Scientist 64:41-45

Maynard-Smith, J. and G. Price
1973 The logic of animal conflicts. Nature 255:219-220.

Miller, G. S.
1931 The primate basis of human sexual behavior. Quarterly Review of Biology VI:379-410.

Parker, G. A.
1974 Assessment strategy and the evolution of fighting behaviour. Journal of Theoretical Biology, Volume 47.

Platt, J. R.
1964 Strong inference. Science 146:347-353.

Popp, J. and I. DeVore
in press Aggressive competition and social dominance theory. In The Behavior of the Great Apes. D. Hamburg and J. Goodall eds. New York: Holt, Rinehart and Winston.

Popper, K.
1959 The Logic of Scientific Discovery. New York: Basic Books.

Ransom, T. W.
1971 Ecology and social behavior of baboons (Papio anubis) at Gombe National Park. Unpublished dissertation. Berkeley: University of California.

Rowell, T.
1966 Forest living baboons in Uganda. Journal Zoology 147:344-364.

1967 Quantitative comparison of the behavior of a wild and a caged baboon group. Animal Behaviour 16:585-588.

1972 Social Behaviour of Monkeys. Kingsport: Penguin Books.

1974 The concept of social dominance. Behavioral Biology 11:131-154.

Sokal, R. and F. Rolhf
1969 Biometry: The Principles and Practice of Statistics in Biological Research. San Francisco: W. H. Freeman.

Stoltz, L. P. and G. S. Saayman
1970 Ecology and behaviour of baboons in the Northern Transvaal. Annals of the Transvaal Museum 26:99-143.

Strum, S.
m.s. Polyadic male aggression in baboons: How not to Lose.

Washburn, S. L. and I. DeVore
1961 Social behavior of baboons and early man. In Social Life of Early Man, S. Washburn ed., Chicago: Aldine.

Yerkes, R. M. and A. W. Yerkes
1929 The Great Apes. New Haven: Yale University Press.

Zuckerman, S.
1932 The Social Life of Monkeys and Apes. London: Kegan Paul.

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