

Table III. Proportion of Agonistic Bouts Won Within Dyads (Total Agonistic Bouts)

Winner	Winner						
	RA	BS	ST	BR	SU	RD	CA
RA	—	0.63	0.78	0.88	0.75	0.74	0.68
BS	—	—	0.78	0.69	0.65	0.66	0.52
ST	—	—	—	0.79	0.94	0.90	0.85
BR	—	—	—	—	0.71	0.58	0.79
SU	—	—	—	—	—	0.53	0.67
RD	—	—	—	—	—	—	0.65
CA	—	—	—	—	—	—	—

are the most closely matched males. The dominant individual of the dyad should win proportionately more as the rank difference between individuals widens. This is not the case. Furthermore, the outcome of an interaction between any pair of males was not certain because many reversals occurred. A reversal was defined as a change in the identity of the winning male in the subsequent encounter between the pair. The dominant male in 10 of 21 dyads won fewer than 70% of the encounters with each of his opponents, and the dominant male in only 2 of 21 dyads won more than 90%. Surprisingly, the highest-ranking male (RA) does not have the highest proportion of total wins when all wins and losses are considered (Table IV), although the two systems for measuring rank are usually thought to produce identical results; nor do the two kinds of rankings closely correspond for other males.

Therefore, while I conclude that a male agonistic dominance hierarchy is present in PHG, it is characterized by numerous reversals and poor predictability of outcome in any given instance. The dominant males within dyads seldom won a large majority of the encounters with the subordinate males. These unusual features may, however, be an artifact of pooling agonistic bouts across the dimensions of time and context.

Table IV. Proportion of Total Wins

	Male							Total
	RA	BS	ST	BR	SU	RD	CA	
Proportion of total wins	0.68	0.54	0.72	0.41	0.28	0.31	0.30	
Total number of bouts	431	542	431	186	250	370	268	1239 (2478 + 2)
Dyadic dominance rank	1	2	3	4	5	6	7	
Proportion rank	2	3	1	4	7	5	6	

In order to ascertain whether this was the case, I first analyzed the data within shorter time intervals. Here agonistic bouts were assigned to successive 3-month periods. Second, I analyzed the data by resource context. Table V presents a comparison of the results which suggests that hierarchies based on subsets of agonistic interactions are similar to those constructed from the pooled data (labeled the "overall hierarchy"), although some aspects of the pattern of interactions do vary.

It is necessary to explain some of the terms and concepts I have applied to the data. Landau (1951a,b) devised a measurement of the linearity of a hierarchy, "h." To be strictly linear, the rankings within a hierarchy must be transitive, that is, if A dominates B and B dominates C, then A must also dominate C. However, departures from this rule are common in animal groups. DeVore's (1965) concept of the central hierarchy identified the importance of these kinds of modifications in linear rankings for male baboons. DeVore focused on the ability of C to dominate A by means of coalitions with B, or with another male. However, circularities in rankings can occur without coalitions and Landau's index extracts the amount of linearity that is present in a hierarchy, from 1.0 (perfectly linear, totally transitive, no circularities) to 0.0 (completely nonlinear, nontransitive, and with frequent circularities).

Another aspect of hierarchical relationships is the degree to which one animal dominates another. Because reversals were common among PHG male baboons, two measures of the frequency of reversals were made. The number of stable dyads (i.e., where the dominant member won all of the bouts) was compared. The amount of "consistency" was also compared by dyad, and for each hierarchy when all dyads were averaged. Consistency will be used as a shorthand term for "the proportion of wins by the dominant male in the dyad." When the proportion of wins is low (as the value approaches 50%), the winning is more inconsistent. As the proportion of wins for the dominant individual increases, the consistency increases until reaching 100%, where one of the two males always wins.

We can now consider the significance of using shorter time intervals to evaluate agonistic dominance. Rankings were constructed in a manner identical to that for the overall hierarchy. First, the dominant male within a specific dyad was determined (the male of the dyad who won the largest proportion of encounters during that time period). Then all males were ranked on the basis of the number of other males to whom they were dominant. Dividing all agonistic bouts into quarterly time periods yields several interesting results (Table V). For example, there are more dyads which are stable, especially in quarter 1 (two males immigrated into PHG during quarter 2). Despite this, Landau's *h* is lower in each quarter than in the pooled data; in other words, the rankings are all less linear. Shortening the time intervals does not seem to result in more consistent rankings. The hierarchies in all but quarter 1 correlate significantly with the

Table VII. Agonistic Bouts, Predation Context ($N = 348$)

Winner	Winner							Total
	RA	BS	ST	SU	BR	RD	CA	
RA	—	13	1	2	3	19	11	49
BS	3	—	47	5	1	28	12	96
ST	0	0	—	31	20	70	11	132
SU	0	3	1	—	1	12	5	22
BR	0	2	1	0	—	4	0	7
RD	3	10	4	6	0	—	9	32
CA	0	6	1	2	0	1	—	10
Total	6	34	55	46	25	134	48	348

time periods or by resource context does not produce a dominance hierarchy significantly different from that obtained when the data were pooled. The majority of dyads remains unstable, reversals are still common, and linearity declines rather than increases. However, the context of agonistic interactions does seem to exert some influence on the patterning of male interactions within the hierarchy.

Agonistic Dominance Hierarchy: Significance

I have demonstrated that an agonistic dominance hierarchy, with some characteristics not common in other data, exists in the data on PHG male baboons. The criteria for dominance that I have used to produce linearity (i.e., who won 51% or more of the agonistic bouts), do, however, obscure what is basically a highly variable set of dyadic interactions. But does this dominance hierarchy have a biological or adaptive significance? In previous studies the importance of an agonistic dominance hierarchy has been interpreted in terms of the priority-of-access model and ultimately related to a male's reproductive success (DeVore, 1965; Hausfater, 1975; Seyfarth, 1975; Hamilton, 1978; Packer, 1979). A positive correlation has been found between high dominance rank and acquisition of resources, particularly among estrous females (but see Gartlan, 1968; Bernstein, 1970; Rowell, 1974).

Before discussing the adaptive significance of the PHG male dominance hierarchy, it is necessary to assess whether dominance rank does correlate with acquisition of resources for PHG baboons.

Acquisition of Resources

I consider the relationship of agonistic dominance to resource acquisition in terms of estrous females and prey items, for the reasons given earlier.

Estrous Females

A behavioral assessment of a male's reproductive success is difficult if not impossible. A male's monopoly of an estrous female has reproductive significance only if he fertilizes the female. For the purposes of my analysis I have chosen to use the number of consorts rather than other measures of reproductive success, because copulations occurred at a low frequency and consorts were not followed continuously, making assessment of actual time spent in consort unreliable. Furthermore, copulation rate and consort rate were highly correlated for males, when project data from a 3-year period were examined ($r = 0.9950$, $N = 603$, $P = 0.0028$), making consort data a reliable substitute for the less numerous data on copulations.

The point at which conception is most likely during a female baboon's cycle is still a controversial issue (Hendrickx and Kraemer, 1969; Wildt *et al.*, 1977), but days D-3 to D+1 (days are counted from detumescence of a female's sexual swelling) appear reasonably to bracket the period. The cycle in which conception occurred can be retrospectively determined from a female's cycle and information on the offspring's date of birth. I have labeled this the "cycle of fertilization" in the discussion that follows.

During the study period there were 225 days with at least 1 female observed in estrus (Table VIII), though only 119 of these days also had one or more consort pairs. In all, 381 consorts were observed. There were twice the number of consort partners for a female during the cycle of fertilization than in either of the previous two cycles. Four of the 12 females impregnated during the study period had consorts only during this cycle. There was an increase in the number of consort partners a female had during cycle days D-3 to D compared with other cycle days, during both the cycle of fertilization and the two preceding cycles (chi-square test— $df = 3$, $P = 0.001$, $N = 381$).

With these data, PHG males can be ranked according to the proportion of consorts they obtained during their stay in the troop (Table IX). Although an overall ranking was easy to determine, consort rank in the two cycles preceding the cycle of fertilization did not predict consort rank in the fertilization cycle, since only the male with the greatest number of consorts remained consistent.

Priority-of-access predictions about how dominance rank correlates with consort activity are contradicted by the PHG data. There is no positive correlation between agonistic dominance rank and reproductive activity. In fact, there is a

Table VIII. Number of Estrous Females Simultaneously Available [Following Hausfater (1975)]

	0	1	2	3	4	5	Total
Number of females	0	1	2	3	4	5	
Number of days	97	94	91	28	10	2	322
Percentage of total	30	29	28	9	3	1	100

Table IX. Adult Male Ranks in Consorts, with Highest Rank as Number 1 (*N* = 381)

Total consorts	
Male	Rank
SU	1
CA	2
BS	3
RD	4
BR	5
RA	6
ST	7
Cycle of fertilization	
SU	1
CA	2
RD	3
BS	4
RA	5
ST	6
BR	7
Nonfertilization cycles	
BS	1
SU	2
RD	3
CA	4
BR	5
ST	6
RA	7
D-3 to D	
SU	1
RD	2
BS	3
CA	4
BR	5
ST	6
RA	7

negative trend (Table X): high-ranking males are the least frequent consort males and obtain the smallest proportion of estrous females.

Inconsistencies between male baboon dominance rank and reproductive activity have been previously noted by Hausfater (1975), Seyfarth (1975), and Packer (1979). They found that while consorting activity was significantly correlated with dominance rank, the alpha males did not monopolize all of the fertile females available to them. One explanation which has been offered is that dominant males are more "selective" in their choice of females, preferring particular

Table X. Dominance and Consort Rank Correlations (Consorts, *N* = 381)

Dominance rank	Consort rank	Correlation		
		<i>N</i>	<i>r_s</i>	<i>P</i>
(1) Yearly total agonism	Yearly total	7	-0.57	>0.05
(2) Quarterly total	Quarterly total			
(a) 1st quarter		5	-0.1	>0.05
(b) 2nd quarter		7	0.18	>0.05
(c) 3rd quarter		7	-0.5	>0.05
(d) 4th quarter		7	-0.57	>0.05
(3) Yearly total	Cycle of fertilization and two previous cycles			
(a) Total	Total consorts	7	-0.67	>0.05
(b) Total	Consorts, D-3 to D	7	-0.79*	<0.05
(4) Yearly total	Cycle of fertilization			
(a) Total	Total consorts	7	-0.47	>0.05
(b) Total	Consorts D-3 to D	7	0.04	>0.05

* Significant.

females even when other estrous females are available. While agonistically high-ranking males in PHG are also consorting with a smaller proportion of females than low-ranking males when all consorts are considered (*N* = 7, *r_s* = 0.255, *P* > 0.05), no males in PHG, including those of highest rank, showed the extreme selectivity in consorting with specific females that Hausfater found. Furthermore, the male ranked as alpha in agonistic interactions, while being low-ranking in consorts (fifth lowest of seven males), was the second least selective male in choice of females available to him.

One aspect of male "selectivity" in consorting may relate to the rank and the potential reproductive success of females. However, Packer (1979) found that consorting selectivity by males was not correlated with a female's dominance rank. Likewise, males of all ranks in PHG distributed their consorting between females of all ranks.

Consorting selectivity might also result from female choice (Saayman, 1971) arising from relationships between males and females outside the consort setting (Saayman, 1971; Ransom, 1971). For PHG males and females, nonsexual affiliation was determined by examining the grooming and following interactions of each male and female. A female who follows a male during her anestrus periods and grooms that male in preference to other available male partners (and at times in preference to kin partners) has been classified as affiliated to that male. Females can be affiliated to more than one male at any given time, and the degree of affiliation was measured by the proportion of grooming time and following time devoted to each male. Males frequently initiate affiliation with females. Each male's grooming and following activities were similarly analyzed and combined with the data from females. Among PHG males there is a sig-

Agonistic Dominance in Male Baboons: An Alternative View

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Data on baboons have generated both the concepts normally associated with male dominance hierarchies among primates and the tests of their significance. The priority-of-access model has been used to predict the relationship between dominance rank and resource acquisition. While the correlation between these two factors, or between rank and measures of reproductive success, has varied among different primate species, most recent baboon field-workers have interpreted their results to be consistent with the model. Based on 1200 hr of observation of a troop of savannah baboons near Gilgil, Kenya, this paper presents data on male agonistic interactions and on male acquisition of resources. Predictions of the priority-of-access model are tested and an inverse relationship is found between agonistic dominance rank and acquisition of two limited resources, estrous females and meat. The importance of the residency status of males is explored and an alternative hypothesis is presented to account for the anomalous pattern in the data. The relationship of male reproductive success and dominance rank is evaluated in light of the data on these baboons and the "residency" hypothesis.

KEY WORDS: baboon; dominance; reproduction; migration.

INTRODUCTION

Dominance and dominance hierarchy are central concepts in interpretations of primate behavior (recent reviews of the topic, see Gartlan, 1968; Bernstein, 1970, 1976; Rowell, 1974; Wade 1977). However, there has been a long con-

trovery over the subject. The issues include whether dominance hierarchies actually exist, whether both males and females have similar types of dominance interactions, whether a male dominance hierarchy is central to the social organization of the group, whether dominance is a social or a genetic characteristic of the individual, and finally whether dominance has evolutionary significance.

Altmann's (1962) priority-of-access model (or similar but less formalized ideas) has been used as a framework for evaluating male dominance behavior, particularly by baboon field-workers (see Hausfater, 1975; Seyfarth, 1975; Hamilton, 1978; Packer, 1979). Altmann's model predicts that when estrous females are in limited supply, they will become available to males according to the dominance rank of the male, with highest-ranking males taking precedence. The model provides a simple and testable hypothesis about the relationship of male dominance rank to male reproductive success. By extension, male dominance rank has also been linked to the acquisition of any resource of limited availability. Recently Popp and DeVore's (1979) reevaluation of social dominance extended the priority of access model to include a cost-benefit analysis of aggressive competition. They suggest that the type of resource is important to the outcome of an agonistic interaction.

Male dominance hierarchy has been repeatedly offered as a candidate in the search for a descriptive, predictive, and evolutionary explanation of social behavior. But each attempt has met with objections that the concept is not as global or heuristic as its advocates claim (see Gartlan, 1968; Rowell, 1974; Bernstein, 1976), and considerable evidence has always existed which contradicts the general case. Rowell (1966) noted that her forest-living male baboons did not exhibit patterns of agonistic dominance like those reported for some savannah-living groups of the same species and suggested that dominance may be habitat or resource specific. Although he was instrumental in generating widespread acceptance of dominance hierarchy concepts, DeVore (1965) noted that male dominance interactions in the baboon groups he observed were not strictly linear and suggested the importance of polyadic interaction (the central hierarchy). More recently Kummer *et al.* (1974) demonstrated that possession of a female (by establishing a relationship) takes precedence over dominance interactions between hamadryas males, and Hausfater (1975), Seyfarth (1975), and Packer (1979) each noted that the top-ranking males in their baboon groups did not conform to the predictions of the priority-of-access model relative to estrous females, although the model seemed generally to fit these data.

Many factors may contribute to the irregularities and variation found in the data on male dominance hierarchies. For example, dominance hierarchies have been constructed based on different criteria (see Bernstein, 1970), which may explain some of the reported variation. Analyses of field data have favored agonistic behavior because contact aggression is relatively rare, and because other measures such as mounting, presenting, and grooming are not well cor-

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related with each other or with the directionality of aggression. Sometimes agonistic behaviors of differing intensities are pooled. Hausfater (1975), for example, found that for *Amboseli* baboons the intensity of the agonistic behaviors did not substantially change the direction of outcome in a bout. Sometimes aggressive behavior is eliminated entirely as a criterion; Packer (1979) based his male dominance hierarchies on supplanting interactions because of the infrequent occurrence of aggressive behavior for males in three troops of baboons that he studied at Gombe National Park.

Since dominance hierarchies are normally constructed from the total of wins and losses in the outcome of interactions, the time dimension and context are removed. For each pair of interactants, the individual that wins more often than it loses is said to be dominant. The rank of every animal is determined either by the number of others that it dominates or by the proportion of all interactions that it wins. If context plays a role in determining outcome, some of the variation in patterns of male dominance may result from differing contexts of interactions between studies.

Aside from difficulties inherent in measuring agonistic dominance, discussions of the significance of dominance hierarchies include assumptions which may bias the interpretation. For example, when behavioral signals of dominance are used as a substitute for measures of success in acquiring resources, the test of the hypothesis becomes circular. It is also usually difficult to assess conflicting claims about the significance of dominance because the contextual data for dominance interactions are limited, as are data on the methods by which resources are actually acquired. Finally, it is only recently that male dominance interactions have been considered within the context of a male's life history (Rowell, 1972; Hausfater, 1975; Popp and DeVore, 1979; Popp, 1978), an important complicating variable.

Some of the discrepancy in the significance assigned to male dominance is clearly the result of how dominance has been scored and analyzed in the past. But however this is done, agonistic dominance rank must also be demonstrated to predict who gains limited resources. I will, in this paper, reassess the concept of male dominance hierarchies by addressing the following set of questions:

- (1) Does a male agonistic dominance hierarchy exist when all data are pooled irrespective of time and circumstances?
- (2) If it exists, how consistent is it?
- (3) Is the hierarchy more consistent when shorter time intervals or specific resource contexts are identified?
- (4) Do these data conform to the predictions of the priority-of-access model?
- (5) Is there an alternative hypothesis that provides better predictions about the relationship between male dominance rank and acquisition of resources?

These questions are addressed using information collected on one troop of baboons. I end by reviewing the possible adaptive consequences of agonistic interactions and dominance rank within the life cycle of a male baboon.

METHODS

The data for this analysis are based on a field study I conducted of a 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 area is described elsewhere (Blankenship and Qvortrup, 1974; Harding, 1973).

Observation of the focal troop (PHG) began in 1970. In 1973 the troop averaged 7 adult males, 19 adult females, 14 juveniles, and 13 infants. Age classes follow Rowell (1967) and Ransom (1971); however, males are classified as physically adult at 9–10 years and older (rather than 6 years of age) and as subadults at from 5 to 9 years (rather than 4–6 years) based on animals of known ages.

During 1200 hr of direct observation on PHG I used several techniques of data collection, following Altmann (1974). I sampled all individuals 4 years of age or older as focal subjects for predetermined 15-min periods. Additional *ad lib.* sampling provided data on other social interactions, intertroop encounters, predatory behavior, and daily copulations, consorts, female sexual states, injuries, and demographic changes.

The data reported here consist of agonistic bouts (from December 1972 to January 1974) between PHG adult males. During this period three adult males transferred into PHG; one transferred at the beginning and two transferred from the same troop within a week of each other in May 1973. Before May, one adult male died, and the only subadult males in the troop emigrated to another troop. One adult male who transferred and stayed only 1 month is not considered here. The four other adult males had been in PHG since 1970 when observations began, although one of these was a subadult in 1970 that just reached physical maturity in 1972. It is likely that these males transferred from another troop some time before that.

To distinguish the two cohorts of adult males from each other, I have classified those continuously with the troop for less than 1 year as "newcomers" and those who have been with the troop longer than 1 year as "residents."

An agonistic bout is defined as a sequence of behaviors that includes any of the behaviors listed in Table I. When agonistic behaviors were continuous, only one bout was scored, even for lengthy sequences. A bout was considered terminated when the actors no longer directed agonistic behaviors towards each other.

Table I. Agonistic Behaviors

Behavior	Description
Aggressive	
(A) Low-intensity aggression	Stare, raised eyebrows, ears flattened, head bob, yawn, molar grind, ground slap, broken grunting, pant grunt [see Hall and DeVore (1965) for detailed description]
(B) Medium-intensity aggression	Some combination of elements in A
(C) High-intensity aggression:	Lunge, chase, charging run, aggressive contact [See Ransom (1971) for detailed description]
Submissive	
(A) Fear face, geck, tail up, scream, crouch	See Ransom (1971) for detailed descriptions
(B) Others	
(1) Active avoid	Direct movement away from another individual; orientation is obvious but no vocal or gestural communication accompanies movement
(2) Active avoid: moderately fearful	Avoid with rapid movement and repeated glances or fear face or geck or tail up
(3) Active avoid: fearful	Running away with combination of geck, scream, fear face, and tail up
(4) Approach: moderately fearful	Oriented approach with tail up or fear face or geck
(5) Approach: fearful	Oriented approach with tail up and fear face, geck, or scream
(6) Counterattack	Counter chase with submissive elements

The different sampling procedures provided four data files on male agonistic interactions. Male agonistic bouts were retrieved from 156.5 hr of 15-min focal-animal samples on seven males (from March 1973 to January 1974). These are the first data file.

During focal samples, social interactions of the type recorded for the focal animal were also recorded for all animals within 50 ft of the focal animal. Male agonistic interactions from 600 hr of these "focal context samples" comprise the second data file.

Thirteen months of daily *ad lib.* records were screened for male interactions as the third data file.

Normal sampling was routinely interrupted for baboon predatory episodes (Strum, 1975, 1976, 1981), where narrative data on all interactions were recorded. Agonistic encounters between males from 100 episodes of predation are included in the fourth data file.

The winner and loser of each agonistic bout were scored. The procedure and criteria for determining winners or losers were similar to those of Hausfater

(1975, p. 25). When one animal directed only submissive or only aggressive behavior toward another animal, the former was scored as the loser and the latter as the winner in that encounter. When *both* animals simultaneously gave aggressive and submissive gestures towards the other, the outcome was scored as undecided. An agonistic interaction was also scored as undecided when the two actors repeatedly alternated between aggressive and submissive gestures toward each other during the same bout. Less than 1% of all male dyadic agonistic bouts were undecided in outcome by these criteria.

RESULTS

Agonistic Dominance Hierarchy: Does One Exist?

In testing whether an agonistic dominance hierarchy existed for PHG male baboons, I first pooled all agonistic behaviors, thus removing time and context as variables in the interactions, as done by previous investigators. However, I had difficulty constructing a male hierarchy from either the focal-sample data ($N = 336$) or the combined focal-sample and *ad lib.* data ($N = 580$). For these data, rank within some dyads was indeterminate because the two partners had equal wins and losses. Assigning linear rankings for all males was further complicated by the amount of circularity within specific triads. Nevertheless, by combining all data files ($N = 1239$), I could produce a 7×7 matrix that resembled previously described linear hierarchies (Table II). Within a dyad an individual was scored as dominant when he won more than 51% of the bouts with the other male. Rank among all males was determined by the number of males that an individual dominated. This hierarchy exhibits several unusual characteristics; while the hierarchy is linear, the probability of winning is irregular (Table III). The lowest proportion of wins would be expected along the diagonal, as these

Table II. Total Agonistic Bouts ($N = 1239$)

Winner	Winner							Total
	RA	BS	ST	BR	SU	RD	CA	
RA	—	152	25	22	36	31	28	294
BS	91	—	56	29	33	58	24	291
ST	7	16	—	37	81	114	57	312
BR	3	13	11	—	10	14	26	77
SU	12	18	5	4	—	16	14	69
RD	11	30	12	10	14	—	39	116
CA	13	22	10	7	7	21	—	80
Total	137	251	119	109	181	254	188	1239

Table V. Comparison of Different Agonistic Rankings (Time and Resource Considerations)

	Quarterly				Estrous females	Meat
	1	2	3	4		
Dyads without interactions	0	0	0	0	3	1
Number of stable dyads	0	2	1	2	9 of 18	6 of 20
Linearity						
(1) Circularity in dyads	2	1	2	0	2	1
(2) Equality in dyads	2	1	0	2	3	0
Landau's h^*	0.2000	0.5355	0.8211	0.7140	0.2856	0.8925
Number of rank changes from overall rankings	2 of 5	None	5 of 7	4 of 7	5 of 7	1 of 7
Sequential real rank changes	NA*	4 of 5	5 of 7	5 of 7	NA	NA
Correlation with overall hierarchy	NA	$r_s = 1$	$r_s = 0.71$	$r_s = 0.89$	$r_s = 0.75$	$r_s = 0.94$
Comparison of ranking methods, total wins/dyad rank	NA	($P < 0.05$)	($P < 0.05$)	($P < 0.05$)	($P < 0.05$)	($P < 0.05$)
Degree of consistency (SD)	3	3	4	6	1	Same
Resident-resident dyads	$\bar{X} = 0.61$	$\bar{X} = 0.73$	$\bar{X} = 0.71$	$\bar{X} = 0.69$	$\bar{X} = 0.82$	$\bar{X} = 0.72$
Resident-newcomer dyads	(0.07)	(0.11)	(0.11)	(0.18)	(0.20)	(0.10)
Newcomer-newcomer dyads	$\bar{X} = 0.75$	$\bar{X} = 0.77$	$\bar{X} = 0.77$	$\bar{X} = 0.74$	$\bar{X} = 0.76$	$\bar{X} = 0.85$
	(0.11)	(0.15)	(0.11)	(0.15)	(0.22)	(0.29)
	$\bar{X} = 0.82$	$\bar{X} = 0.83$	$\bar{X} = 0.84$	$\bar{X} = 0.84$	$\bar{X} = 1.00$	$\bar{X} = 0.97$
	(0.06)	(0.14)	(0.17)	(0.15)	(0.00)	(0.03)

* Not applicable.

overall hierarchy (Table V), although they correlate with each other in only two cases (quarters 2 and 3— $r_s = 0.714$, $N = 7$, $P = 0.05$; quarters 2 and 4— $r_s = 0.883$, $N = 7$, $P < 0.05$).

Considering agonistic bouts within specific resource contexts, we might predict that the outcome may be related to the cost and benefit of the interaction for the participants (Wilson, 1975; Popp and DeVore, 1979). If this is so, then reversals observed within dyads might have a contextual basis. I have separated agonistic bouts into two contexts, reproduction and predation. These bouts involved resources both restricted in supply and for which the baboons evinced great interest, namely, estrous females and meat. Agonistic interactions occurred less frequently in male rivalry over other resources, such as preferred and limited plant foods, or over anestrus females, proximity to infants, and the like. A large proportion of agonistic interactions did occur where no resource was obviously concerned (see discussion below).

Agonistic bouts around females in estrus ($N = 110$) were retrieved primarily from focal-context samples with additional events from focal samples and *ad lib.* data. These were considered separately from agonistic bouts related to the consumption of prey ($N = 348$) which were retrieved primarily from narrative data on predatory episodes with additional events from focal samples, and focal-context samples.

Although the actual hierarchies constructed from the contextual data (Table VI and VII) correlate significantly with the overall hierarchy and with each other ($r_s = 0.857$, $N = 7$, $P < 0.05$), the context does appear to influence the patterning of male interactions. For example, there are more dyads in which the males do not interact. Dividing the total interactions into smaller quarterly samples did not produce this result, suggesting that the explanation cannot simply be the smaller sample size. There are also more dyads which are stable, particularly in the agonistic interactions around estrous females. Despite this, the linearity of the hierarchy is lower than in the overall hierarchy.

In conclusion, an analysis of the data on agonistic interactions either by

Table VI. Agonistic Bouts, Consort Context ($N = 110$)

Winner	Winner							Total
	RA	ST	SU	BS	BR	CA	RD	
RA	—	1	10	3	0	3	4	21
ST	0	—	2	6	6	3	12	29
SU	4	0	—	3	0	3	2	12
BS	9	3	0	—	3	2	5	22
BR	0	0	0	3	—	0	5	8
CA	3	0	0	1	0	—	2	6
RD	4	0	1	7	0	0	—	12
Total	20	4	13	23	9	11	30	110

nificant positive correlation between the number of affiliated females that a male had and his consort rank ($N=7$, $r_s=0.75$, $P<0.05$), although agonistically high-ranking males sometimes, but not necessarily, selected affiliated females as consorts.

In summary, PHG males that were agonistically high-ranking had fewer consorts and consorted with a proportionately lower number of available females than males that were agonistically low-ranking. However, high-ranking males were less selective on key days during the cycle of fertilization. They also had fewer affiliated females than low-ranking males and they did not necessarily select affiliated females for their consort partners. No high-ranking male in PHG exhibited the extreme "selectivity" reported for some other baboon groups.

The inadequacy of PHG male agonistic dominance rank to predict reproductive activity correctly is inconsistent with expectations based on the priority-of-access model, but to a degree it is similar to previous applications of the model to male baboons. Yet explanations of the behavior of high-ranking males from previous studies do not satisfactorily resolve the issue for these data.

Meat

A second test of the relationship between male dominance rank and acquisition of a resource is provided by data on meat-eating. PHG male baboons in 1972–1974 were unusually predatory for nonhuman primates, taking the young of antelope species, hares, and birds (Strum, 1975, 1976, 1981). The importance of meat to a baboon's diet is still unknown, but by comparison with other major food items meat is a resource of limited availability and one in which PHG males showed considerable interest.

There are various measures that can be used to assess a male's success at getting meat, but in these data none are positively correlated with his dominance rank (dominance versus carcass consumption, $r_s = -0.36$; scrap consumption, $r_s = 0.0$; proportion of kills attended at which some meat was obtained, $r_s = -0.25$; success at getting meat, $r_s = 0.32$; $N=7$, $P>0.05$ in all cases). When the dominance rank is compared to the number of kills made by each male, a negative correlation is found between agonistic rank and capture rate ($N=7$, $r_s = -0.86$, $P<0.05$), a result similar to that found between dominance rank and consort rank. However, order of access to females was not the same as order of access to meat (capture— $r_s = 0.464$, $N=7$, $P>0.05$; carcass feeding— $r_s = 0.321$, $N=7$, $P>0.05$).

In conclusion, although a male agonistic dominance hierarchy can be constructed for PHG baboons and it is linear, dominance rank does not predict who actually possesses either of the two most limited resources, estrous females and meat. In fact when a correlation between rank and resources exists, it is negative. Are there alternative factors that might better predict the acquisition of limited resources for PHG males?

Dominance Hierarchy and Male Residency

The males in PHG can be classified as "residents" or "newcomers" based on the length of time they had resided in the troop. To find the relationship of "residency" to agonistic interactions, the data were treated as in the previous analyses, first irrespective of context, then in the context of estrous females and meat.

In the analysis of residency status and agonistic interactions, newcomers win significantly more than expected when the data are pooled, disregarding time or context (chi-square test— $df=1$, $N=1239$, $P<0.001$). The three newcomers (RA, ST, BR) rank as numbers 1, 3, and 4 in the hierarchy, with the newly matured resident male (BS) as number 2. Furthermore, the distribution of agonism across residency dyads is not random (chi-square test— $N=1239$, $df=20$, $P<0.001$). There is a trend for the resident–newcomer agonistic rate to be higher than the resident–resident agonistic rate, but this falls short of a significant value because of the large standard deviation in individual dyad interaction rate within each category. There is more inconsistency in resident–resident than in resident–newcomer dyads ($t = -2.74$, $df=14$, $P<.005$; variances are not significantly different— $F=2.29$, $f_1=11df$, $f_2=5df$, $P>0.05$) or in newcomer–newcomer dyads ($t=4.40$, $df=7$, $P<0.005$). We can generalize that length of residency is tied to agonistic dominance rank in the following way: newcomers are the high-ranking males and residents are the low-ranking males. The second-ranking male is technically a resident, however, this is a special case of the newcomer phenomenon (see discussion below).

Does this pattern hold when only agonistic bouts involving either estrous females or meat are considered? In the context of estrous females, newcomers no longer win more than expected (chi-square test— $N=110$, $df=1$, $P<0.10$) but the hierarchical ranking remains the same. Newcomers win in agonism around meat as they do in the pooled data (chi-square test— $N=348$, $df=1$, $P<0.001$).

Residency status is tied to agonistic dominance rank in two resource contexts in a manner similar to that for the pooled data. However, residents may do relatively better when a limited resource is at stake (see, for example, the data on agonism around estrous females).

Acquisition and Residency

Given that there is a link between residency and agonistic ranking in PHG, what is the relationship between residency and acquisition of resources? As in the preceding analysis, this question is considered in the context of estrous females and prey items.

Newcomers consort less frequently with estrous females than expected (chi-square test— $N=381$, $df=1$, $P<0.001$) and they occupy the lowest three ranks

Table XI. Demographic Status and Consorting Behavior

Males	Percentage			
	Demography	Consorts	Aggressive turnover when consort δ is	Following by males when consort δ is
Resident	57	79	72	73
Newcomer	43	21	28	27

for consort activity (Table IX). This result is consistent with the inverse relationship between dominance rank and reproductive activity noted in the previous analysis.

Further, while the number of consorts was related to residency, the loss of a consort to another male or the following of a consort by other males was not. Males were followed, or lost their females, in direct proportion to the number of consorts they had (Table XI). Follower males did not selectively attend to consorts of males of a particular residency status. This was true during the entire study period, and there was no increase in aggression or following during the cycle of fertilization, nor was the aggressive turnover rate related to the rank of the consort female ($r_s = 0.09$, $N = 14$, $P > 0.05$).

Newcomers also rank below residents in all measures related to the acquisition of meat. Sixty-one prey were captured by adult males in PHG during the study. Of these, residents were the captors in 77% while newcomers accounted for 23%. On the average, a PHG male fed on a prey carcass at 26% of all consumptions ($N = 100$); however, the mean for a resident male was 33%, whereas that for a newcomer was 17%. Most striking is the comparison of figures on mean success rate for obtaining meat at a kill. A male obtained some meat at 56% of all prey consumption episodes when averaged over all males in the troop. The mean success rate for resident males was 71%, however, while that for newcomers was 36%.

We can conclude that for PHG males the length of residency in the troop predicts both the outcome of agonism and the acquisition of resources. While newcomers win in most agonism, residents obtain the most resources, whether it is estrous females or meat. This explains the negative correlation between dominance rank and acquisition of resources reported in the previous section.

DISCUSSION

While an agonistic dominance hierarchy can be constructed for PHG male baboons, the predictions of the priority-of-access model are not met. These results suggest that a reevaluation of existing ideas about the relationship of agonistic interactions, dominance, and resources is needed (see Bernstein, 1976).

More specifically, we need to consider why there is a dichotomy in agonistic interactions between residents and newcomers, and why, despite losing agonistic encounters, residents still manage to acquire the resources.

I start by evaluating the significance of agonistic interactions; next I consider the methods employed by PHG males to acquire resources; and finally, I consider how resource acquisition tactics are related to a male's length of residency in the troop. I present an alternative hypothesis to explain the anomalous pattern in the PHG data, suggesting that agonistic interactions can be used for purposes not immediately related to competition for limited resources, and that resources can be acquired by means other than aggression.

The Resident–Newcomer Dichotomy in Agonistic Interactions

Agonistic interactions are a method of communication between individuals (see Manning, 1972; Hinde, 1974; Alcock, 1975). Traditionally, the communication was thought to be about competition over a preferred resource, but any communication has social, historical, and physical contexts that can give broader or different meaning.

For PHG baboons, agonism is sometimes used in the course of competition between individuals, but not always. It is not unusual for the winner of a fight between two PHG males to walk away without claiming the resource, although no one has taken it or is limiting the winner's access to it. In this case, whether a behavior is used to signal priority over a resource cannot be inferred simply from the fact that it occurs within a resource context. Newcomer males in PHG use agonistic interactions as one means to integrate themselves into the troop, a method by which information about and relationships with other males are acquired.

A transfer male both observes and interacts with the members of his new troop during his initial period of social adjustment. By employing the two techniques he acquires social knowledge and experience, but only by interacting can he establish relationships within the group.

A newcomer initiates relationships with troop females by following them, one at a time, maintaining close proximity, and through grooming. The sequence closely resembles sexual consorts but without copulations. Females are not aggressively coerced, probably because for olive baboons the response to aggression is an increase in the distance between the interactants (cf. Kummer *et al.*, 1970). Eventually the female assumes joint responsibility for maintaining the relationship as she follows, grooms, and stays close to the male. This becomes a "special" relationship, a term applied to a similar pattern for male and infant pairs (Ransom and Ransom, 1971). The affiliations between male–female pairs are apparent in subsequent grooming preferences and in the aid-seeking and aid-giving behavior of individuals during aggression and during consorts.

Although affiliation among male olive baboons is rare, a relationship of sorts is established between individual males. This is initiated in a manner similar to that for females, but the methods differ. While following one male at a time, a newcomer makes frequent approaches that can include greetings or harassments. The majority of interactions is agonistic. Successive males are followed in the same way. Ransom (1971) describes one such sequence for a transfer male at Gombe Stream Reserve.

The circumstances of these adult male interactions frequently do not involve a dispute over a resource; even in resource contexts, the "goal" of the interaction for the newcomer is rarely the resource. Continual following, harassment, and aggression by newcomers occur irrespective of the outcome of the previous episode, and the resource item is seldom claimed. The goal appears to be both an assessment (Parker, 1974) of the other male (B. Smuts, personal communication) and a method by which the target male is forced to recognize the newcomer's presence in the troop. This explains why the majority of agonistic bouts has no resource context and also explains the trend for increased agonistic interactions between newcomers and residents. Other baboons employ agonistic interactions similarly. For example, when a juvenile male reaches adolescence (about 4 years of age) he aggressively provokes females higher-ranking than his mother. These interactions persist irrespective of resource contexts, yet they cease entirely once the female capitulates and the dominance ranks between the two baboons reverse. Although there may be some long-term benefit in terms of resource acquisition, there are no immediate resource gains in these kinds of agonistic interactions for either newcomers or juvenile males.

Maturing males are a special case of the "newcomer phenomenon." Whether natal or immigrant, they attempt to *change* their existing relationships with group members (both males and females) to be more consistent with their new developmental status. They use the same techniques as those just described for adult male immigrants.

Why Do Residents Get the Resources?

If a proportion of PHG male agonistic interactions are not related to competition over resources, how are resources acquired? Evidence from PHG baboons suggests that where competition is appropriate, individuals may use alternatives to aggressive strategies. These depend, to a great extent, on an individual's ability to assess complex social situations and to manipulate aspects of these situations to its own benefit. I refer to such instances as "nonaggressive" or "social" strategies of competition (for fuller discussion, see Strum, Social strategies and the evolutionary significance of social relationships, Unpublished manuscript). Data on PHG consorts provide a useful illustration.

There were 119 days when I observed at least one consort pair in the troop.

Aggression around consorts occurred during 36 of these days. In the 325 different consortships where I observed a change in consort partner, only 26% were the result of aggression between successive consort males. The majority of turnovers could be classified as the successful use of a social strategy (Strum, in preparation).

For example, as tension mounted between a consort male and other males following the consort pair, a turnover might occur. The new consort male was frequently not one of the active followers, but rather a male that had remained uninvolved and that had closely monitored the situation from a distance. At the appropriate moment, he would rush the female and claim her without any agonistic interactions with the other males. On other occasions, a male might incite others against the consort male while remaining uninvolved himself. When all the males were otherwise occupied, the inciting male would claim the consort female.

Affiliation with females, outside of the consort context, played an important role in male success during consorts, and these affiliations represent another class of social strategy (Strum, in preparation). To be successful reproductively, a male must initially solve two problems. First he must acquire access to an estrous female, generally as the outcome of aggressive competition between males (Mayr, 1972; but see above). But access does not guarantee insemination of that female. Although a male baboon, by virtue of his larger size, can and often does force his consortship onto a female, rape does not occur. Inseminating a female depends on her cooperation. Female choice (Mayr, 1972) is clearly implicated in PHG male social strategies and in male reproductive success. At times a male will voluntarily give up his consort female if she has consistently prevented him from copulating or has increased the opportunity costs of the consortship to a point where he is no longer able to sustain the effort. A female will exercise her "choice" further by approaching a male of her preference to initiate a new consortship. The influence of female preferences, particularly for affiliated males, was evident in subtle and diverse ways in many consort situations. Females were qualitatively most cooperative and least disruptive to a male's behavior when they were in consort with an affiliated male (Strum, in preparation). At these times, the female helped to maintain proximity between the pair, sometimes reversing the normal olive-baboon consort situation where the male follows the female.

Having an affiliation with his consort partner also gives a male an advantage during harassment by follower males. The male can depend on the female to maintain proximity and so need not divide his time and attention between returning aggression to the followers and preventing the female from running off. The ability of a consort male to retain his female during an aggressive challenge could depend largely on the cooperation of the female.

Although males who were most reproductively active in PHG were not

selective in their choice of females, consorting as they did with both affiliated and nonaffiliated females, the costs of each type of consortship visibly differed. The potential success in insemination is likely to have differed as well. The number of female associates that a male had (outside of the consort context) significantly correlated with his ranking in consorts, suggesting a relationship between the two that lends support to the present argument.

Using the consort data as an example, aggression may not be the only, the most frequent, or even the most effective form of competition between PHG males. A male who fights to get a female, only to have her be uncooperative, thus preventing him from copulating, may be less reproductively successful than a male who rarely uses aggression but has the ability to accurately assess and manipulate the social situation. This ability is based on social experience and on preexisting social relationships.

Besides the relative *success* of the two types of strategies, the *costs* of aggressive competition may be higher than that of nonaggressive alternatives. This involves two types of costs: real risk of injury and opportunity costs.

Among Amboseli baboons, consort pairs avoid aggression by moving away from the troop (Hausfater, 1975). Consort pairs in PHG normally stay within the troop but may try to move away in response to aggression by follower males. The followers pursue the pair; males sustain more wounds when estrous females are present in the troop. Wounds to adult males represent more than that expected from the total number of wounds observed and the demography of the troop (chi-square test— $df = 1$, $N = 42$, $P < 0.001$). The daily wounding rate for males is significantly higher when consorts are present than when they are not (arcsin angular transformation— $t = 18.75$, $P < 0.0001$).

The cost of consorting can also be viewed in terms of opportunities foregone in some other activity such as feeding. Social strategies such as long-term affiliations with females or the "watch-wait-rush in" tactic can have the effect of reducing these kinds of opportunities costs to the male.

Where social strategies of competition exist, are effective, and in some cases are more successful than aggressive alternatives, resources may be acquired through nonagonistic methods. But social strategies require an initial investment of time in determining the social dynamics of the troop and in establishing the necessary social relationships. Resident males have what newcomers lack, the basic information and social networks from which social strategies can be developed.

Tactics of Newcomers

A new male's obvious attempts to establish relationships within his adopted troop probably have reproductive benefits. The formation of relationships with

females may result in greater reproductive success by increasing opportunities for copulations, reducing costs to the male while in consort, and heightening his effectiveness in countering aggressive challenges to his consortships. These relationships provide the male with the option of deploying less risky, and more effective, social strategies. Adults must be distinguished from adolescent male immigrants in terms of the effectiveness of these newcomer tactics. Mature male immigrants have the skills but lack the current social knowledge to use social strategies. Adolescent males have some rudimentary knowledge because they have resided in the troop for a period of time before becoming sexually active. But in making the transition to adulthood, they have yet to perfect the necessary techniques and still must gain experience in using them appropriately.

While forming relationships with females seems to have tactical significance for newcomers, the advantage of interacting with resident males is more problematic, particularly when access to resources is not correlated with agonistic dominance. Still, a newcomer could need to acquire knowledge about resident males for a number of reasons, for example, to use within the context of aggressive competition. During the times when consort turnovers are the result of aggression, it would be important to assess correctly when and with whom to compete aggressively. And a general knowledge of the characteristics of other males is necessary for effective social strategies as well. While observing social interactions does provide a new male with useful information, it is a slow process. Information can be accumulated more quickly through interacting with individuals. Beyond the testing of capabilities and limitations, interacting provides a means to influence the attitudes of other males. For a new male, these agonistic interactions with other males may accelerate the process of integration into the troop.

An Alternative Hypothesis

The prediction that agonistic dominance rank correlates with access to resources rests on several assumptions. First, the function of aggression is competition between individuals; second, dominance hierarchies result from individual differences in aggressive/competitive abilities; third, resources are of limited availability; and finally, competition between individuals for limited resources is by means of aggression (or agonism), with the agonistic winner obtaining the contested item. When one, or a combination, of these conditions is not met, there will be an imperfect fit between dominance rank and the acquisition of resources.

An alternative hypothesis can be deduced from the data on PHG baboons. This hypothesis states that a male agonistic dominance hierarchy will reflect the dynamic interplay of the structure and stability of male membership in the group with the relative availability, benefits, and costs of different strategies of com-

petition. The degree of correlation for male baboons between an agonistic dominance hierarchy and the acquisition of resources will vary as resources, residency profiles, and male competitive strategies vary.

This hypothesis assumes the following:

- (1) There are nonaggressive strategies of competition as effective as, and potentially less risky than, aggressive strategies.
- (2) Deployment of these social strategies depends on an individual's social experience and knowledge of the troop and on an established set of social relationships.
- (3) Males that are new to a troop do not have the necessary prerequisites to use most social strategies.

All other things being equal, if a group has a period of stable male composition (with no maturing adolescent males), and no alternatives to aggressive strategies of competition, then the limitation of resources will primarily determine the frequency of male agonistic interactions. The correlation between dominance rank and access to resources should be strong (see Fig. 1).

For the purpose of simplicity, I consider that all resources represent the same costs and benefits to the individual actors. Popp and DeVore (1979) discuss specific predictions about the relationship between aggression and resources where costs and benefits vary.

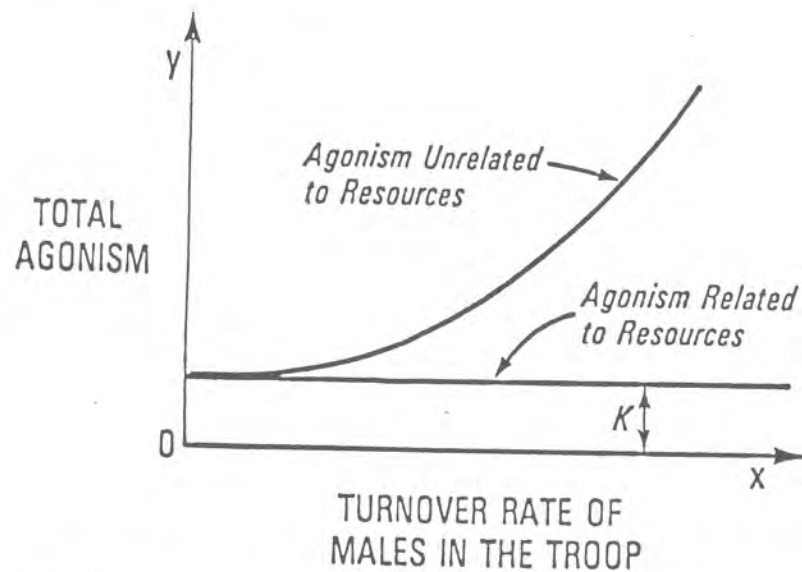


Fig. 1. Hypothetical profile of male agonistic interactions (stable environment with K = constant amount of interactions related to competition for resources).

If male membership is not stable, and resources are limited, and if there are no alternatives to aggressive strategies of competition, then two distinct agonistic hierarchies should occur: one in resource contexts, where agonistic rank predicts acquisition of the resource (but residency class may not predict agonistic rank); and one in the context of male interactions unrelated to resources, where residency status of males determines agonistic rank (e.g., newcomers are high-ranking, etc.) but these agonistic ranks do not subsequently predict access to resources. The two agonistic dominance hierarchies should not correlate with each other.

If male membership is in flux and resources are limited, and alternatives to aggressive strategies exist, then some general predictions can be made, although more detailed predictions depend on the specifics of the resource and residency situation. Resident males should have a greater access to limited resources than new immigrant males. Immigrants should initiate and win most of the agonistic interactions unrelated to resources. Residents should employ a combination of aggressive and social strategies of competition (with an emphasis on social strategies for appropriate resources), while immigrants should employ primarily aggressive strategies (severely limiting their access to some resources). The strategy of immigrants should change with the length of residency in the troop to approximate that of "residents" more closely. Since adolescents have to acquire both techniques and knowledge in order to use social strategies, mature male immigrants should be integrated into the troop more readily and come to approximate the behavior of resident males more rapidly than adolescents. Dominance rank will not necessarily be an accurate predictor of resource acquisition. However, as the male turnover rate in the group decreases, existing agonistic interactions should be more closely linked to aggressive competition (see Fig. 1). Dominance rank will then increasingly correlate with acquisition of certain resources.

Male Reproductive Success and Dominance Rank

Rowell (1972) has suggested that dominance is an age-related phenomenon for primates and all males will eventually assume all ranks equalizing the variations between males observed at any one point in time. Hausfater (1975) interprets his data on dominance and reproduction to suggest that the amount of time a male stays in particular dominance ranks will determine his overall reproductive success. While I concur with Rowell's suggestion that dominance is related to a male's life cycle, the evidence from PHG males and the "residency hypothesis" suggests an additional possibility. Because most male baboons leave their natal troop sometime during adolescence (e.g., Packer, 1979; Strum, in preparation) and continue to transfer between troops during adulthood, a troop's male membership is normally in flux. This creates a natural continuum in re-

residency status between males in the troop, similar to that observed among PHG males in 1973, and consequently differential access to resources based on the residency status of the males. As a result, a male's ultimate reproductive success can fluctuate greatly depending on his idiosyncratic history of emigration and immigration, the male residency structure in each troop he joins, and the length of time he remains in each troop.

Although a male's reproductive success is constrained by his transfer behavior, it is possible that a male might advantageously manipulate these constraints through his choice of troops and the timing of each event. To be effective, a male would need to assess two variables: the relative resource availability in the different troops (for example, the number of females, the density and distribution of foods, etc.) and a comparison of the residency structure in each of the troops. Together these determine his *potential access* to resources and his *potential success* in acquiring those resources. On this basis he can make choices about immigration that maximize his relative chances for reproductive success. Although the usual disclaimer of conscious decision-making by the animal must be included at this point, the actual behavior of male baboons in the study population dictates that this be only a partial disclaimer. These males show great interest in other troops during interactions: sitting and watching the other animals, attempting to greet males in the other troop, etc. Furthermore, males in the process of transferring between troops usually monitor several troops and may join different groups for short periods before making a permanent transfer.

Adult-male transfer events should be distinguished from adolescent transfer events. Adult males are more likely than adolescents to make choices based on assessment. Adolescent males will be influenced, to a greater extent, by hormonal changes and, since they lack previous experience, will encounter more difficulty making choices about when and where to immigrate based on assessments.

CONCLUSIONS

Traditionally, the dominance hierarchy concept was considered useful because it provided the means to predict behavior over time, across contexts, and in ways that were imputed to have evolutionary significance. But to model male dominance and its significance, simplifying assumptions had been made which necessarily reduced the complexity inherent in the real behavior. Subsequently, the developing paradigm led to the conclusion that the system itself was simple. Exceptions were treated as anomalies to be disregarded rather than providing evidence of an underlying complexity for which the existing concepts could not account.

The current study adds to a growing body of data that indicates the limitations in the heuristic value of the concept of dominance hierarchy, at least for male baboons. Revisions have previously been proposed; these have been mod-

ifications of specific applications of the concept or the substitution of related concepts. For example, Rowell's most recent critique (1974) suggests that a "subordinant hierarchy" would be more useful than the concept of a dominance hierarchy. She also illustrates the potentially artifactual nature of dominance interactions. Bernstein (1976), following Gartlan (1968), makes dominance a social role that is only partly related to aggression. He emphasizes the influence of social skills, especially skills in the initiation of aggressive coalitions upon which the alpha male's power rests. Bernstein suggests that social rather than aggressive factors may play an important part in primate groups.

Investigators who retain much of the original dominance concept place new limitations on its applicability. For example, Popp and DeVore's (1979) treatment of dominance adjusts hierarchies to specific resources through a cost-benefit model of aggressive competition. Hausfater (1975) and Packer (1979) restrict the concept by introducing the ideal of alpha-male "selectivity" (at least in reproductive behavior) to account for the unorthodox pattern of mating among the highest-ranking males in their respective troops. Hausfater further suggests that while dominance ranks may have closely correlated reproductive success, no one individual can be identified with any particular rank since many individuals occupy each rank during short periods of time.

The data from PHG baboons suggest that further reassessments of the dominance concept are required. It is particularly clear that the significance of male agonistic dominance must be evaluated relative to numerous factors. Concepts and models more sophisticated than those previously advocated are required. These must consider that, first, agonistic interactions can have more than one function, requiring that behavioral signals be clearly separated from interpretations of their meaning (e.g., agonistic behavior from interpretations of resource acquisition).

Second, collapsing the contexts within which behaviors occur probably obscures important patterns of agonistic interactions and information about their significance. Even in the PHG data where the influence of context on agonistic rank was minimal, the type of resource seemed to affect male interactions. Viewing agonistic interactions as social communication also demands that all possible contextual meanings be evaluated. These minimally include the social, historical, and resource factors for each interaction.

Third, residency patterns are critical to an understanding of male interactions, agonistic or otherwise. Differences in life-cycle stages between males (and their different life histories) will strongly influence which behaviors they exhibit and the significance of those behaviors (Rowell, 1972; Popp and DeVore, 1979). Life cycle, life history, and male migration are all inextricably linked in an evolutionary complex. But the immediate consequences are at the social level and are expressed in terms of a residency continuum that confers differential knowledge, relationships, and competitive abilities on males and which each male enters anew each time he changes groups.

And, finally, alternatives to aggressive competition exist for nonhuman primates living in complex social groups. Manipulation of social knowledge and relationships can replace dominance and status in the social dynamics of PHG baboons (Strum, unpublished manuscript).

At best, then, agonistic dominance is only part of a male's lifetime attempt to maximize his reproductive success. If the residency hypothesis is correct, the link between agonistic dominance rank and reproductive success is variable and potentially weak, and consequently the concept of male dominance hierarchy has less evolutionary importance.

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