



Long-Term Consistency of Dominance Relations among Female Baboons (*Papio cynocephalus*)

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as high as this (median, .20). The last figure is comparable to that found for trial 1 and trial 2 approach orders to unchanged nonfood objects (5). These results are as one would expect if marmosets (like humans) remember self-generated information better than information from others (11). The marmosets may have deferred socially to those who had initially discovered the food, but a more parsimonious hypothesis is that the discoverers were the most discriminating and eager.

Differential response to the two classes of objects was still very clear on the retention trial ($P < .01$ on each measure). Most food objects evoked food calls as soon as they were sighted; no nonfood object did. With nonfood (but not food) objects the number of days elapsed between trials 3 and 4 and the amount of time spent on or in the apparatus were correlated ($r = .69$, $P < .05$); either these objects tended to be forgotten eventually or the animals simply rechecked even old and unproductive objects after enough time had elapsed. Here, both win-stay and lose-shift performances could be viewed as special cases of varying optimal return time (4). Obviously, animals do not stay indefinitely at a food object but rather leave and return after a time or when the object in question has probably replenished its food supply.

In subsequent experiments we have replicated all of the above findings in a variety of contexts, including tests with no food reward after the trial of discovery, with simultaneous presentation of as many as 30 test objects, and with test objects behind a visual blind (in which case some group members took their cue exclusively from a leader). We do not predict how the same animals would do if tested in social isolation in an unfamiliar cubicle with more customary learning set procedures. It would be surprising, however, if free-ranging members of this species are incapable of the same sorts of performances reported here. Why they might be so skilled is an open question. Even 1-month-old infants have an effective strategy for obtaining solid foods, namely, "Take your cues, if not the food itself, from others." As long as any family member is curious enough to check new objects and tolerant enough of food sharing or stealing, and food is sufficiently abundant, others fare well. It is no doubt when social strategies are insufficient for them that individuals lose-shift and use asocial or antisocial strategies instead (12). Not only for *S. fuscicollis* as contrasted with other species but also for infants as contrasted

with adults, the most pertinent question for students of foraging is not how they compare in general learning ability or intelligence but rather what sorts of problems each animal faces and what strategies are sufficient for solving them (3, 4).

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1. Only one callitrichid (marmoset), *Callithrix jacchus*, has to our knowledge been tested on the standard experiment of this sort. [R. C. Miles and D. R. Meyer, *J. Comp. Physiol. Psychol.* **49**, 219 (1956)]. Its trial 2 performance stayed at a chance level for more than 200 problems and reached an asymptote of 75 percent correct after roughly 1000 problems.
2. H. F. Harlow, *Psychol. Rev.* **56**, 51 (1949); in *Psychology: A Study of a Science*, S. Koch, Ed. (McGraw-Hill, New York, 1959), vol. 2, p. 492; J. M. Warren, in *Comparative Psychology*, D. A. Dewsbury and D. A. Rethlingshafer, Eds. (McGraw-Hill, New York, 1973), p. 47.
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4. For recent reviews of foraging theory, see A. C. Kamil and T. D. Sargent, Eds., *Foraging Behavior: Ecological, Ethological and Psychological Approaches* (Garland, New York, 1981); J. R. Krebs, in *Handbook of Behavioral Neurobiology*, P. Marler and J. G. Vandenbergh, Eds. (Plenum, New York, 1979), vol. 3, p. 225. Probably the strongest single set of evidence against the view of learning set theory (2) that one-trial learning of visual discriminations requires much training and is a good cross-species index of intelligence is recent research on insects [for example, R. Menzel and J. Erber, *Sci. Am.* **239**, 102 (July 1978)].
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7. The reason for this gradual introduction of food and of randomization of object presentation orders is that for most animals, *S. fuscicollis* included, the odds of finding food on any particular object or in any specific location less than a half cubic meter in size must be small—and any large departure from normative odds might be expected to produce over-responding and breakdown of lose-shift behavior. Our animals, however, were little affected by 50 percent reward and randomized orders of object presentation. In the next experiment, trial 2 discrimination of food from nonfood objects was still better than chance over 40 objects presented four at a time, one trial per object per day, with intertrial intervals of a few minutes and (overall) no differential reward for win-stay or lose-shift performance.
8. The female parent died suddenly of undetermined causes during week 1 of phase 4. Her data are excluded from trial 4 and from Fig. 1E. All results remain essentially identical.
9. We exclude from Fig. 1 and from the statistical analyses the two so-called food objects on which the animals never discovered the food.
10. *Saguinus fuscicollis* have highly developed olfactory and scent-marking systems [G. Epple, in *Primate Behav.* **4**, 195 (1975)]. Precautions taken included control tests in which food or food odors were placed in objects toward which the animals were previously habituated. Responses were no different from those to an unbaited object until the animals came within a few centimeters of the object. Scent-marking of the test objects was seldom observed.
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13. We thank G. Epple of the Monell Chemical Senses Center for lending us the animals.

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Long-Term Consistency of Dominance Relations Among Female Baboons (*Papio cynocephalus*)

Abstract. At maturity, female baboons in the Amboseli National Park of Kenya generally attain a rank position among adults near to that of their mothers. However, the age of a female's mother and the difference in ages between sisters also influence the rank acquisition process. These latter demographic variables, which are sensitive to changes in resource availability, may account for the close association both within and among primate species of specific patterns of rank organization and specific environmental conditions.

Long-term studies of provisioned and captive macaques have shown that at maturity a female generally attains a dominance rank position immediately beneath that of her mother and above that of her older sisters (1). We have observed the dominance relations among adult females in a wild population of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park of Kenya for a comparably long term. Our analysis of

the ranks of identifiable females in our main study group, Alto's group, is based on 10 years of observations, an interval roughly equal to the adult life expectancy of a female baboon (2, 3). The data support the prevailing notion that for many species of Old World monkeys the rank of a daughter at maturity is strongly influenced by that of her mother. However, examination of the case histories of Amboseli baboons suggests that the rank

of a female at maturity is also influenced by the age of her mother, the intervals between her birth and the births of her sisters, and other demographic factors of her group. These findings help explain both reported variation (4) in female ranks among primate species as well as the way in which potentially adaptive modifications of group organization take place in response to changing environmental conditions.

Basic definitions and scoring procedures for agonistic behavior among Amboseli baboons were established in 1971 at the start of our longitudinal study (5). During the initial 14-month study period, dominance relations among the 11 adult females in Alto's group were stable: the outcomes of more than 99 percent of all agonistic bouts ($N = 656$) were consistent with a simple linear ranking of adult females (5). Five of the 11 females survived into 1977 and their ranking relative to each other in that year was the same as it had been during the 1971–1972 study period (Table 1, females MO, LU, PR, SC, and OV). In fact, during each year of study and over longer periods of time, rank relations among the adult females in Alto's group have shown a high degree of consistency (Table 2).

In addition to the stability of rank relations among fully adult females in Alto's group, the Amboseli data show that at maturity, daughters generally attain rank positions among adults close to those of their mothers (Tables 1 and 2). In most cases, daughters began to establish their adult rank around age 4, approximately 1 year before menarche, and completed their entry into the adult dominance order by 5½ years, nearly 1 year before the birth of their first offspring (2, 3, 6). For example, Table 1 includes four females of known maternal affiliation (daughters of AL, FL, and RI) who were 1 to 3 years of age in 1971–1972. By 4 years of age, each of these immature females had begun to dominate one or more older females, and by 1976 each had attained a rank position among adults nearly identical to that of her mother in 1971–1972 (Table 1). Furthermore, analysis of the case histories of these four females, as well as those of females who subsequently matured (6), has shown that the attainment of maternal rank was not solely dependent on any single variable such as survival of the mother, interventions by kin, completion of physical growth, or large body size (5, 6).

As a result of the strong influence of maternal rank on the rank of offspring, dominance relations among Amboseli females show a high degree of consistency

Table 1. Outcome of decided agonistic bouts among adult females in Alto's group from August 1976 through October 1977. The value in a cell is the number of times the animal in that row (dominant) won an agonistic bout with the animal in that column (subordinate). The 1971–1972 rank order in this group was SK, TT, AL, MO, LU, FL, PR, SC, OV, JU, and RI (5). Daughters are designated by the mother's initials followed by a "d"; relative birth order of daughters is indicated by subscripts: 1, 2, and 3. Data were obtained by two (or occasionally three) independent observers for 343 days.

Dominant	Subordinate													
	AL-d ₁	MO	LU	FL-d	PR	SC	RI-d ₁	RI-d ₂	SL	OV	HA	PL	BR	ES
AL-d ₁		42	22	22	44	22	23	10	11	40	13	10	6	15
MO			14	20	16	19	14	13	22	33	26	25	12	12
LU				28	16	15	21	19	22	11	15	24	10	5
FL-d					28	16	24	21	11	24	27	19	9	9
PR						11	12	13	15	15	12	11	10	5
SC							18	11	8	24	4	10	4	4
RI-d ₁								36	25	14	31	42	13	8
RI-d ₂									40	14	24	41	14	18
SL										60	8	27	15	6
OV											19	23	19	12
HA												32	17	16
PL													37	22
BR														3
ES														

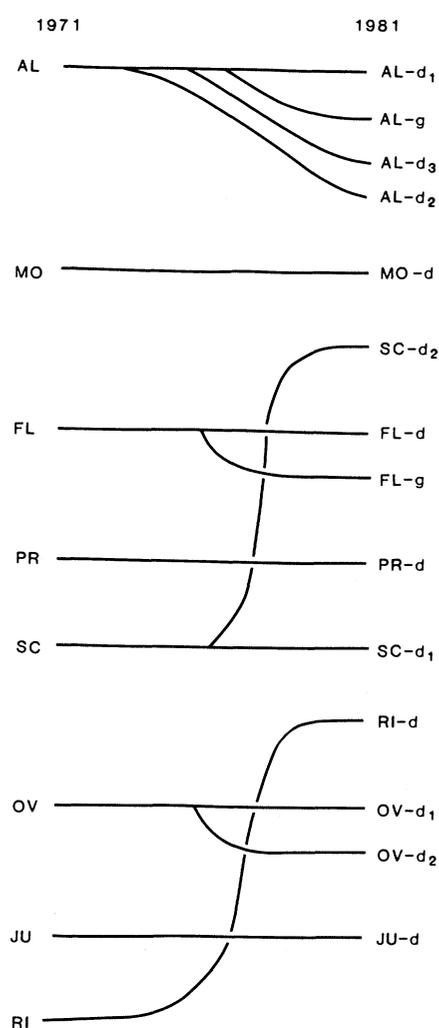


Fig. 1. Relative ranks of adult females in Alto's group in 1971 and of their adult female lineal descendants in 1981. Related females are identified as in the legend to Table 1. AL's daughters were born in 1970 (estimated), 1973, and 1975; SC's daughters in 1973 and 1975; OV's daughters in 1973 and 1976. Complete genealogies are described by Altmann (2).

not only between successive years of study but also between successive generations. Eight of the 11 adult females present in Alto's group in 1971 (Table 1) were survived by 14 adult female descendants whose relative ranking in 1981 (Fig. 1) shows that, in all but two cases, the relative ranks of descendants corresponded to those of the 1971 matriarchs. To date, most short-term studies of baboons have emphasized the significance of adult male dominance relations in group organization (7). Our longitudinal study has revealed that rank relations among females are consistent both within and between generations and thus may represent the single most important source of long-term stability and continuity in group organization.

Even in the few cases in which a daughter attained a rank above that of her mother, there was a close correspondence between the mother's and daughter's ranks. These exceptional cases are associated with specific events or conditions that indicate some factors other than the mother's position that influence rank acquisition by maturing females. First, the rank attained by a maturing female is influenced by the age of her mother. Three females in Alto's group (daughters of PR and SC) eventually became dominant over their mothers (Table 2), but in all three cases the mother was at least 15 years old and had begun to show marked physical and behavioral signs of advanced age. We hypothesize that as females advance in age they become increasingly less likely to constrain or "cap" the rise in rank of their maturing daughters (for example, RI-d₁, in Table 1 and SC-d₂ in Fig. 1). Advanced age also appears to increase

Table 2. Outcome of decided agonistic bouts among adult females in Alto's group from January through November 1981. The females were observed for 195 days. Granddaughters are indicated by "g" and are listed immediately below their mother. The rise in rank of OV-d₂ and FL-g was still in progress during this 1981 study period; both females were born in the latter half of 1976. Daughters and their birth orders are as described in the legend to Table 1. The value in a cell is the number of times the animal in that row (dominant) won in an agonistic bout with the animal in that column (subordinate).

Domi- nant	Subordinate																			
	AL				MO-d	SC-d ₂	FL		PR-d	PR	SC-d ₁	SC	RI-d ₂	OV		SL	HA	PL	EN	JU-d
	d ₁	g	d ₃	d ₂			d	g						d ₁	d ₂					
AL-d ₁	3	3	5	5	6	3	2	9	8	7	5	8	2	3	10	11	0	4	2	
AL-g		7	19	13	6	2	9	5	10	4	9	7	3	6	6	9	3	4	3	
AL-d ₃			10	3	5	4	2	4	9	2	1	4	2	5	5	2	3	1	2	
AL-d ₂				9	9	3	11	15	6	10	2	7	2	5	3	12	3	6	5	
MO-d					14	0	2	7	6	5	2	3	6	4	5	3	1	5	6	
SC-d ₂						6	5	8	11	8	0	5	0	6	5	5	5	4	2	
FL-d				1			0	12	5	6	3	2	3	3	3	8	2	4	1	
FL-g								3	6	3	4	1	0	9	2	0	0	1	0	
PR-d									0	5	2	7	1	7	6	2	1	5	7	
PR										2	2	1	5	4	2	5	1	3	1	
SC-d ₁											4	2	2	8	7	9	7	3	2	
SC												4	2	1	4	1	1	6	2	
RI-d ₂													6	5	3	3	1	7	6	
OV-d ₁														4	1	3	5	6	3	
OV-d ₂															6	6	3	1	1	
SL																0	1	3	10	
HA							1										9	9	5	
PL							1											12	10	
EN							3												20	
JU-d																				

the probability that a female may decline in rank (for example, JU as of 1973 and OV as of 1975), but not all older females show these patterns.

Second, the difference in age between pairs of sisters determines whether the younger member of the pair will surpass the older in dominance. In sister pairs in which one was at least 2 years older than the other, the younger remained subordinate to the older at maturity (RI-d₁ and -d₂ in Table 1; AL-d₁ and -d₂, AL-d₁ and -d₃, and OV-d₁ and -d₂ in Fig. 1). In the pairs in which sisters were less than 2 years apart in age, the younger did surpass the older in rank at maturity (AL-d₂ and -d₃ and SC-d₁ and -d₂ in Fig. 1).

A third possible factor suggested by the Amboseli records is that the rank position "targeted" (6) by a maturing female is the same as that of her mother in the first year of the daughter's life rather than the mother's rank at some later stage in the daughter's social development. In 1973, shortly after Alto's group merged with a subsidiary study group (8), a low-ranking female from Alto's group, JU, gradually fell in rank below all the adult females in the subsidiary group (SL, HA, PL, BR, and ES in Table 1). The decline in JU's rank was probably age-related, but more importantly it occurred when her daughter (JU-d₁) was less than 1 year of age. Within 2 years' time, a second low-ranking female, OV, also began a gradual decline in rank and by 1978 was subordi-

nate to the same females as JU. This occurred, however, after OV's older daughter (OV-d₁) was 3 years of age. By 1980-1981, when both daughters (JU-d₁ and OV-d₁) were adults (Table 2), OV's daughter ranked above all females from the subsidiary group, but JU's daughter ranked below all of these females.

Demographic influences on rank acquisition have strong implications for understanding the pattern of female dominance relations among baboons and other primate species. For example, were a population such as that of Amboseli baboons to experience highly favorable environmental conditions, one would expect enhanced survival of mothers and their offspring, smaller age differences among sister pairs, and delayed onset of physical signs of aging (9). These demographic changes would in turn influence rank relations and would eventually produce a more strictly genealogical rather than age-ordered (4, 10) pattern of rank relations among adult females. Simulation analysis of demographic influences on dominance relations in baboons has shown that populations in permissive environments will in general be characterized by a degree of nepotism in female rank relations comparable to that of provisioned macaques, but in harsh environments an age-graded rank order of females will emerge (11). In sum, demographic influences on female rank acquisition, as revealed by the long-term study of Amboseli baboons in their natu-

ral and highly variable environment, provide a mechanism whereby correlations between specific patterns of rank organization and specific ecological conditions might arise.

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Uranium Series Ages of the Del Mar Man and Sunnyvale Skeletons

Bischoff and Rosenbauer (1) claim that their uranium series ages for the Del Mar man and Sunnyvale skeletons indicate that the previously published aspartic acid racemization ages (2) of these two skeletons are too old. They state that the concordancy of their ^{230}Th and ^{231}Pa ages supports the uranium series ages for the bone samples. Uranium series ages, however, are based on the critical assumption that bones incorporate uranium for only a relatively short time after their burial and have subsequently remained closed systems with respect to migration of both uranium and its daughter isotopes ^{230}Th and ^{231}Pa . We maintain that the assumption of rapid uranium incorporation followed by closed system behavior is tenuous and that ^{230}Th - ^{231}Pa concordancy is a necessary but not sufficient condition to establish this behavior and thus the accuracy of the dates.

Modern bones contain trace amounts of uranium (3). However, fossil bones assimilate uranium during their depositional history (3). [This was one of the three methods (3) used to demonstrate that the famous Piltdown man actually was composed of both modern and fossil components.] A uranium series age is thus the average integrated age of uranium incorporation into a bone; this age is always less than the bone's actual age.

The processes by which bones acquire uranium are complex (4, 5), possibly episodic (6), and poorly understood. As a result, it is not possible to evaluate the rate of uranium accumulation in any particular bone. Bischoff and Rosenbauer assume that uranium is rapidly incorporated into bones by a mechanism that involves the reduction of uranium by "active (or labile) organic matter." No mechanisms have been presented for this process, nor is it known what organic compounds might be involved. The fact

that fossil bones contain uranium in both the +4 and +6 oxidation states (5) indicates that the mechanism assumed by Bischoff and Rosenbauer does not completely describe how bones assimilate uranium. Moreover, uranium analyses of samples from various stratigraphic units at Olduvai Gorge, Tanzania, have demonstrated that bones and teeth remain an open system with respect to uranium accumulation over periods of hundreds of thousands of years (6, 7).

Bischoff and Rosenbauer state that "it is possible to judge the validity of a uranium series date on a single sample by testing for internal concordancy between two independent decay schemes: $^{238}\text{U} \rightarrow ^{230}\text{Th}$ and $^{235}\text{U} \rightarrow ^{231}\text{Pa}$." In fact, a close examination of the ^{230}Th - ^{231}Pa concordancy diagram shows that, for samples with ages of several tens of thousands of years or less, concordancy is a very insensitive test for the validity of the closed-system hypothesis, especially with regard to uranium uptake. For samples at the young end of the concordancy curve, late uranium uptake can decrease apparent radiometric ages without disturbing ^{230}Th - ^{231}Pa concordancy within experimental uncertainty ($\pm 2\sigma$). For older samples, although concordancy is a better test, what is being dated is the time of uranium uptake by the bone, which is later than their burial time. That the concordancy of ^{230}Th and ^{231}Pa ages is not always a valid indicator of whether the resultant ages were equivalent to the burial age of the sample was first discussed by Kaufman (8), who cited concordant ages of 69,000 and 112,000 years that had been obtained for mollusk shells from marine terrace deposits of apparently the same age. Similar problems have been found for bone (9, 10). For example, in the Middle Pleistocene low-

er stratigraphic units at Caune de l'Arago in the eastern French Pyrenees, concordant (within 2σ) ^{230}Th and ^{231}Pa ages range from $\sim 35,000$ to $\sim 120,000$ years (10).

As has been pointed out by others (3, 9), since the time sequence of uranium accumulation is unknown, even concordant uranium ages are lower limits and should be regarded as minimum ages. Szabo (9) concluded that in some instances concordant uranium series ages for bones can be too young by as much as several tens of thousands of years (11). The uranium series ages given by Bischoff and Rosenbauer for the Del Mar man and Sunnyvale skeletons should therefore be considered minimum estimates, and the actual ages may be greater, possibly by as much as several tens of thousands of years. Such a conclusion is consistent with the racemization ages which have been determined for these skeletons (2).

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11. Since submission of this comment we have obtained some preliminary results in a comparative study of uranium series, amino acid racemization, and collagen-based radiocarbon ages of fossil bones [J. L. Bada and R. Finkel, in *Quaternary Coastlines and Marine Archaeology: Toward the Prehistory of Land Bridges and Continental Shelves*, P. M. Masters and N. C. Fleming, Eds. (Academic Press, London, 1982)]. Our results confirm Szabo's conclusion; concordant uranium series ages were found to be consistently younger than the amino acid racemization and radiocarbon ages, in some cases by as much as 10,000 to $\sim 30,000$ years.
12. We thank H. H. Veeh and our colleagues at Scripps Institution of Oceanography for helpful discussions.

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