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Tail Carriage in Baboons *(Papio cynocephalus)*: Relationship to Dominance Rank and Age

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Abstract. Several metric and categorical variables were used to assess tail carriage in 717 photographs of 54 yellow baboons *(Papio cynocephalus)* of known identity, sex, dominance rank, and estimated or known age. Analyses of these data demonstrated that age was the primary factor, influencing tail carriage of baboons not engaged in social interaction. Specifically, the proximal segment of the tail was carried increasingly close to the vertical with increasing age; other changes in tail angles and segment curvature were also correlated with age. There was no relationship between dominance rank and neutral tail carriage in adult male or adult female baboons, nor was the neutral tail carriage of the first-ranking male or female either distinctive or characteristic. The morphological basis of ontogenetic changes in neutral tail carriage in baboons is also discussed.

Introduction

This paper describes ontogenetic changes in the tail carriage of free-living yellow baboons *(Papio cynocephalus)* in the Amboseli National Park, Kenya. The data for this analysis were 717 photographs of 54 baboons of known identity, sex, dominance rank, and estimated or known age. Every member of a single well-studied group, Alto's group, was photographed an average of 3–4 times/year from 1971 through 1974 as part of an ongoing longitudinal study. The size of Alto's group ranged from about 30 to 50 individuals during this 4-year period. Exact census data for several years and a description of group organization are given by HAUSFATER [1975]; the ecology of Amboseli baboons has previously been described by ALTMANN and ALTMANN [1970].

Baboon tail carriage was of interest in the long-term research program primarily because tail position and shape were physical characteristics that proved extremely useful for recognizing individual baboons. In general those individuals with extremely long or extremely short tails, or other peculiarities of tail shape were the first ones that a new observer learned to identify. Thus, to assure continuity of individual identification for the long-term study, it was necessary to document maturational and other sources of change in tail carriage that might prevent reidentification of individuals after an absence from the field.

Two important factors that could potentially affect tail carriage in baboons were dominance rank and age. Several observers [ALTMANN, 1962; KOFORD, 1963; LINDBURG, 1971; OJHA, 1974] have stated that there is a tail carriage characteristic of the dominant adult male in rhesus monkey *(Macaca mulatta)* groups, a tail carriage almost never used by lower ranking adult males or other monkeys. In contrast, SADE [1971] concluded that the dominance rank of an adult male rhesus monkey could not be determined from tail carriage alone and that no single tail carriage was used exclusively by first-ranking males. Earlier studies of baboons [HALL and DEVORE, 1965; DEVORE, 1962] noted a characteristic stride and air of 'confidence' on the part of the dominant adult male in a baboon group, but gave no information on tail carriage. Thus, the first analyses for this paper examined the relationship of dominance rank to tail position in adult baboons of both sexes and also attempted to determine if there were a tail position characteristic of the first-ranking adult male or adult female.

OPPENHEIMER [1969] has shown that forehead hair coloration and tuft patterns change as a function of age in white-faced monkeys *(Cebus capucinus)*, and it was suspected that baboon tail positions might show similar age-related changes. Thus, a second set of analyses for this paper examined the relationship of tail position and shape to age. Additionally, consistent differences in tail carriage between individuals of different age-sex classes could potentially provide an important and easily visible criteria for estimating the age of individuals of unknown birth date [ALTMANN *et al.*, 1975].

There was also a purely descriptive aspect of this study. In particular, a description of tail carriage in neutral situations, i.e. outside of social interactions, is a necessary precursor to studies of the communicative or signaling function of the tail. Thus, once neutral tail position is established, movements of the tail during social interaction can be described as angular displacements of various tail segments from the neutral baseline yielding more precise descriptions of potentially communicative tail gestures. In sum, the goal of this

study was to complete an accurate and quantitative analysis of neutral tail carriage of known individual baboons and to determine the influence of rank and age on tail carriage; in doing so, this study differs from all previous work on tail carriage in primates which has dealt with the subject only at the most general level [SADE, 1971; OJHA, 1974].

Methodology

Tail position and shape in photographs was described by four metric or angular measurements and four nonmetric or categorical variables. In all cases, the photographs were direct lateral views of an individual baboon standing and feeding, moving slowly between feeding sites, or in a slow spontaneous progression across open savannah. Regardless of precise context, a photograph was included for measurement only when the subject was not engaged in any obvious social behavior. Thus, this paper concerns the neutral tail carriage of baboons, defined as tail position and shape outside of social interaction.

The baboon tail was schematized by using straight lines to specify links or segments of the tail and then by measuring the angles between pairs of segments or between one segment and a horizontal baseline. An approximate horizontal baseline was added to each photograph by drawing a line between the contact points of a hand and foot on opposite sides of the body. This method of tail carriage analysis was of course subject to errors in the measurement of tail angles, tail shapes, and the placement of the horizontal whenever the midsagittal plane of the baboon was not precisely parallel to the focal plane of the camera; however, the magnitude of these errors was probably small compared to the magnitude of other influences on tail position and shape. Also, these measurement errors can be assumed to be distributed randomly, i.e., non-systematically, across year of study, age of subject, and rank of subject. In essence this method of tail position and shape analysis was an application of globographics [PROST, 1967] or the Eshkol-Wachman movement notation system [GOLANI *et al.*, 1969] in two rather than three dimensions.

Angular and metric variables. Figure 1 shows a photograph of an adult female, Preg, prepared for measurement with various tail segments and angles labeled. A curved or angular juncture divided the tail into a proximal and a distal segment. The angle between the proximal segment and the horizontal was referred to as angle 1 and the angle between the proximal and distal segments was referred to as angle 2. Angle 3 was defined by the proximal tail segment and a line in the approximate position of the subject's spine. All angles were measured in degrees and as a convention an angle of 0° was recorded when two segments were parallel to each other. A fourth metric variable measured relative tail segment length and was obtained by dividing the length of the proximal tail segment by the length of the distal tail segment in each photograph. All three of the angular measurements were closely fit by a linear normal distribution and thus use of the Pearson product-moment correlation coefficient and other parametric statistics was appropriate [BATSCHELET, 1965].

Categorical tail shape variables. The four categorical variables included shape of proximal tail segment, shape of distal tail segment, shape of juncture, and tail tip-to-hindlimb projection. The proximal and distal segments were recorded as curving anteriorly, curving

posteriorly, or linear; the tail juncture was categorized as an angular bend, smooth curve, or sharp curve, i.e., an inverted U-shaped juncture, producing almost parallel proximal and distal segments. Lastly, the tip of the tail was projected onto the slightly flexed hindlimb and was recorded as falling above the middle of the femur, between midfemur and knee, from knee to midtibia, or below midtibia.

Age estimation and dominance rank determination. Census categories for baboons and the estimated age range of individuals in each category were originally published by DEVORE [1963], HALL and DEVORE [1965] and ALTMANN and ALTMANN [1970]. Recently, the age ranges for these categories have been modified, at least for the Amboseli population, on the basis of new information on the growth of individuals of known birth data [ALTMANN *et al.*, 1975]. Table I summarizes census categories and lists both the original and revised age estimates for each category. In the analyses that follow, angular and other measurements for each individual have been plotted against the revised [1975] estimates of the lower limit of the age range of the census class of that individual unless otherwise specified.

Criteria of dominance, based on the consistency of outcome of sequences, or bouts, of agonistic behaviors and a description of dominance relationships in Alto's group, have been published by HAUSFATER [1975], and the reader is referred to that work for a more detailed discussion. Briefly, the outcome or winner of dyadic agonistic bouts was determined on the basis of aggressive and submissive behaviors given by the participants and not by priority of access to food or other incentives. The consistency of outcome of successive agonistic bouts for pairs of individuals was evaluated through time, and each individual was assigned a rank based on the number of other individuals consistently defeated in such bouts. In the present study, the dominance rank of individuals was determined by these same criteria or, for 1971 and 1972, taken directly from HAUSFATER [1975].

Results

Correlation of Angular Variables

Initial analysis of the angular variables included calculation of a cross-correlation matrix for all three sets of measurements. This matrix showed that angles 1, 2, and 3 were all highly correlated with each other; the absolute values of the Pearson product-moment correlation coefficients between these variables, taken in pairs, were all above 0.90. Thus, the following discussion will focus on changes in angle 1 with respect to dominance rank and age, and the data for the other two correlated measures will be summarized in tabular form only.

Tail Position and Dominance Rank among Adult Males

Figure 2 is a scatter plot of dominance rank for adult males against angle 1 based on 170 photographs of 14 different adult males who were in Alto's group between 1971 and 1974; however, not all males were present throughout the study. Adult male baboons changed rank frequently [HAUSFATER, 1975],

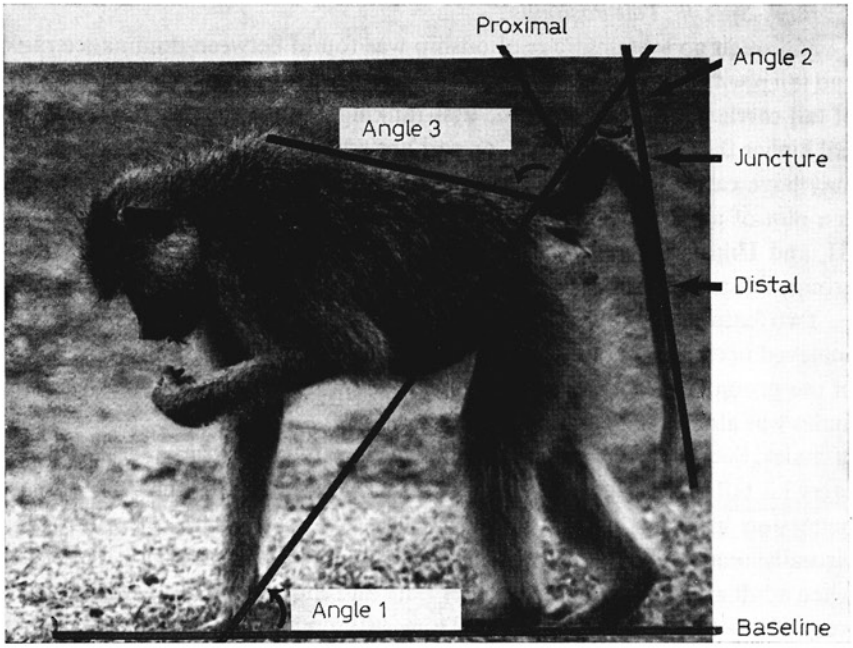

Fig. 1. Photograph of adult female Preg prepared for measurement with tail angles and tail segments labeled. Horizontal baseline was established by drawing a line through the point of contact with the ground of one hand and one foot on opposite sides of the body.

and each point in figure 2 represents the mean value of angle 1 in all photographs of a given adult male taken while that male held the rank indicated on the abscissa. For example, male Stubby occupied ranks 1, 2, 3, and 4 during the study and thus contributed four data points to figure 2.

The least squares regression line (angle on rank) is also shown in figure 2 and has a nonsignificant negative slope. The correlation coefficient between dominance rank and angle 1 was –0.10, not statistical significant from zero correlation. At most then, dominance rank accounted for only 1% of the variance in tail position among adult males. Table II summarizes analyses of the other angular variables with respect to rank and includes correlation coefficients based both on the individual within rank means, as plotted in figure 2, and on the raw data. Use of the raw data on tail angles increased the proportion of variance in tail position accounted for by rank to 9%. Thus, it is clear that dominance rank had no strong effects on tail position among adult males.

Rank-Specific Tail Positions?

Although no systematic relationship was found between dominance rank and tail position for adult males, there may still have been rank-specific modes of tail carriage. For example, the first-ranking adult male may have held his tail higher than any other male, or perhaps any male who assumed first rank may have carried his tail higher than he did when lower ranking. Figure 3 is a plot of angle 1 against dominance rank for three adult males – Stubby, BJ, and High Tail – each of whom was at one time first-ranking in Alto's group, but previously or subsequently held a lower rank.

Two features of figure 3 are noteworthy. First, in general, adult males who achieved first rank did not carry their tails higher than did other adult males in the group. The spread or variation in angle 1 for the three first-ranking males was almost as great as the spread in tail angles within the entire sample of males. Secondly, when a male became first-ranking, he did not necessarily carry his tail higher than when lower ranking. For example, the least squares regression lines in figure 3 show that angle 1 for adult male Stubby was virtually unaffected by changes in his dominance rank; angle 1 decreased when adult male BJ assumed a higher rank and showed precisely the opposite trend for adult male High Tail. Thus, although tail position sometimes changed slightly when an adult male gained first rank, the changes were neither always present nor consistent between males. Examination of the data for several adult males who held the lowest rank in the group, but later moved to a higher rank, also failed to reveal a tail position specific to the most subordinate adult male.

Tail Position and Dominance Rank Among Adult Females

Figure 4 is a scatter diagram of the mean value of angle 1 against dominance rank for 16 adult females who were in Alto's group between 1971 and 1974; a total of 235 photographs of adult females were measured. As among adult males, there is no systematic relationship between dominance rank and angle 1 for adult females; the least squares regression line has a nonsignificant negative slope, and the nonsignificant correlation coefficient of –0.32 indicates that rank accounted for only about 10% of the variance in tail position among adult females. Analyses of the other angular variables, summarized in table II, gave similar results.

Adult female baboons changed rank infrequently compared to adult males and usually only as a result of death or maturation to adulthood [HAUSFATER, 1975]. In fact, ranks 1 through 4 have been held by the same four adult females since late 1971. Thus, it was not possible to analyze data from individual

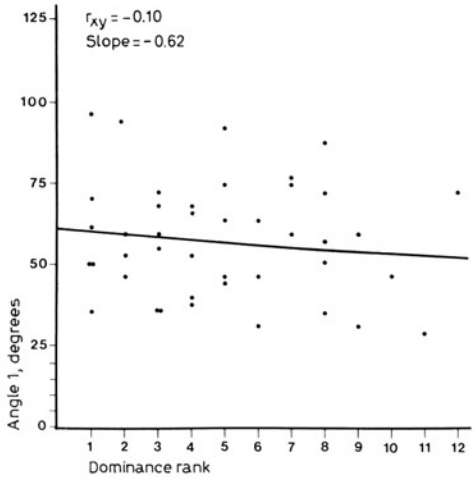

Fig. 2. Scatter diagram and least squares regression line of tail angle 1 (degrees) against dominance rank for adult males. Each data point represents the mean value of angle 1, calculated from all photographs of a given male while holding the rank indicated on the abscissa. See also table II.

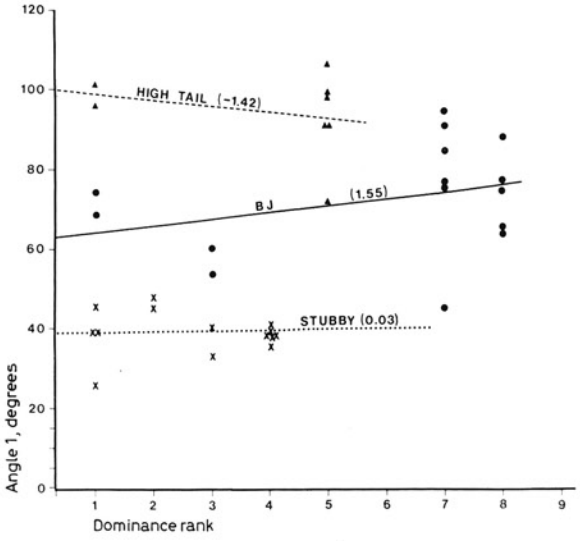

Fig. 3. Scatter diagram and least squares regression line of tail angle 1 (degrees) against dominance rank for three individual adult males who occupied first rank as well as one or more lower ranks during the study period. Number in parenthesis following name of male gives slope of LS regression line.

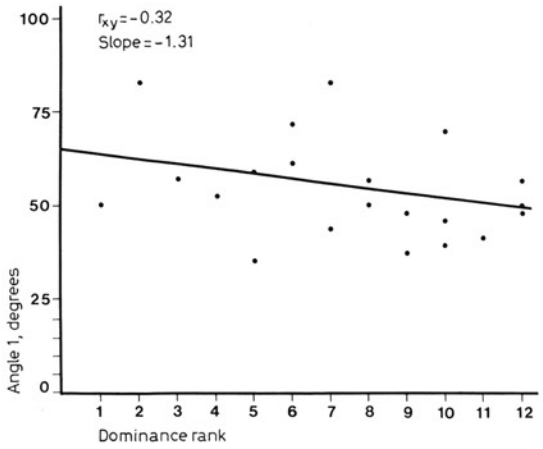

Fig. 4. Scatter diagram and least squares regression line of tail angle 1 (degrees) against dominance rank for adult females. Each data point represents the mean value of angle 1, calculated from all photographs of a given female while holding the rank indicated on the abscissa. See also table II.

females in a manner similar to that used for adult males in figure 3. However, figure 4 gives no indication that either the highest or lowest ranking adult females had a distinctive tail position.

Tail Position as a Criterion of Dominance

The absence of a relationship between neutral tail position and dominance rank among both adult male and adult female baboons does not mean that tail position was an unreliable indicator of the outcome of agonistic bouts. Most catalogues of agonistic behaviors for baboons [KUMMER, 1957, 1968; HALL and DEVORE, 1965; HAUSFATER, 1975] have included 'tail-up' as a submissive behavior. Briefly, a subordinate baboon when hit, bitten, or otherwise threatened by a more dominant individual often raised its tail vertically into the air. In contrast, no threatening or aggressive tail position has yet been described for baboons. Thus, while the tail-up position was a reliable indicator of the submissive or defeated individual in agonistic bouts, and thus a criterion of dominance, tail position in neutral situations gave no information concerning dominance rank or paired dominance relationships.

Tail Position in Relationship to Age

Figures 5 and 6 are scatter plots of angle 1 against estimated minimum age of census class (table I) for 27 males and 27 females, respectively, who

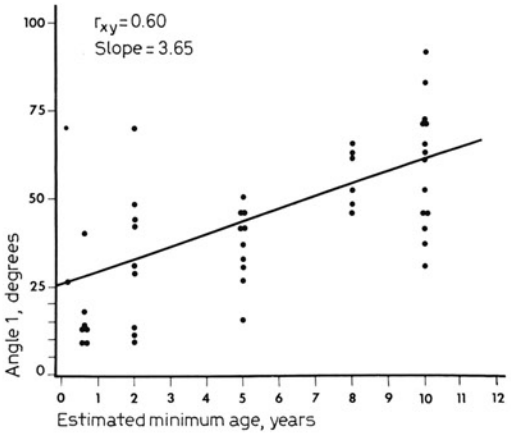

Fig. 5. Scatter diagram and least squares regression line of tail angle 1 (degrees) against estimated minimum age (years) for males. Each data point represents the mean value of angle 1, calculated from all photographs of a given male while in a given census class. Data points are plotted against estimated minimum age of individuals in each census class as taken from table I. See also table III.

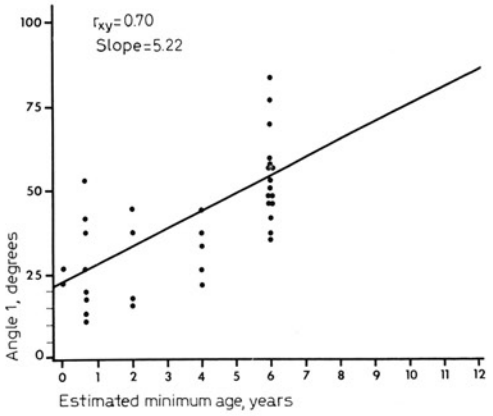

Fig. 6. Scatter diagram and least squares regression line of tail angle 1 (degrees) against estimated minimum age (years) for females. Each data point represents the mean value of angle 1, calculated from all photographs of a given female while in a given census class. Data points are plotted against estimated minimum age of individuals in each census class as taken from table I. See also table III.

were with Alto's group for any length of time between 1971 and 1974. In these figures, each data point represents the mean value of angle 1 calculated from all photographs of a given individual while in a given census class; the estimated lower age limit of the class is shown on the abscissa. An individual that matured from, say, the juvenile-1 class to the juvenile-2 class during the study contributed two data points to these figures, while an individual that was adult in 1971, and thus adult throughout the study, contributed only one data point. The effect on the correlation coefficient of nonindependence of successive data points from the same individual is assumed to be negligible.

Since estimated minimum age as plotted on the abscissa does not correspond precisely to true age, it is obvious that the maximum possible correlation between *estimated minimum* age and angle 1 must be less than 1.00 even if a perfect correlation existed between *true* age and angle 1. Nevertheless, the correlation coefficient between estimated age and angle 1 was 0.60 for males and 0.70 for females, indicating that 36 and 49% of the variance in tail angles for males and females, respectively, was accounted for by age, even when only imprecisely estimated minimum ages were available. Table III summarizes analyses of other angular variables, using both the mean angle within census class for each individual and the raw data, and in all data sets, estimated minimum age accounted for a much larger proportion of the variance in tail angles than did dominance rank (tables II, III).

Another way to look at these data is through examination of the slope of the least squares regression lines shown in figures 5 and 6 and listed in table III. An increase in angle 1 of 3.65° for males and 5.22° for females was recorded for each 1-year increase in estimated minimum age. A total of 11 males and 5 females were represented in two or more census classes and provided a sample of 27 maturations between adjacent census classes. One of the 6 individuals maturing from the infant-2 to juvenile-1 class and 3 of the 11 individuals maturing from the juvenile-1 to juvenile-2 class showed slight decreases in angle 1; no decrease was greater than 5°. All other maturations resulted in increases in angle 1. Despite the failure of these few individuals to increase angle 1 in relationship to advancement in census class, 15 of the 16 individuals, who made at least one census class transition, showed an overall increase in angle 1 across the study period.

In fact, changes in angle 1 were not uniform across census classes. As can be seen from figures 5 and 6, the largest absolute change in angle 1 for both males and females occurred after maturation from the juvenile-2 class into the subadult and adult classes, respectively. Nevertheless, in general, as baboons of either sex increased in age, the proximal segment of their tail

Table I. Description of census classes for Amboseli baboons including original (1970) and revised (1975) age range estimates for each class

Census class	Physical characteristics	Original age estimates, years [ALTMANN and ALTMANN, 1970]	Revised age estimates, years [ALTMANN *et al.*, 1975]
Infant-1	hair completely or partially black (natal coat); skin pink or red from vascularity	0–½	0–⅔
Infant-2	hair brown to cream-colored, often lighter (in Amboseli) than that of adults; skin pigmented black, as in adults	½–1	⅔–2
Juvenile-1	not sharply demarcated from previous class; light hair retained in yellow baboons	1–2	2–4 for females 2–5 for males
Juvenile-2	not sharply demarcated from previous class; hair often darker, as in adult	2–4	4–5 or 6 for females 5–8 for males
Adult female	sexually mature, sexual skin swells periodically; nipples button-like when nulliparous, elongated in more mature, multiparous females	over 4	over 6
Subadult male	development of secondary sexual characters: mantle (in *P. anubis*), long canine teeth, large size, greater musculature than females; scrotum (testes) larger than in juvenile-2	4–6	8–10
Adult male	secondary sexual characteristics fully developed	over 6	over 10

moved closer to the vertical, and these age-related changes in tail position were highly consistent among individuals.

The correlations between estimated minimum age and angles 1–3 were not reduced by even 10% of the values listed in table III when the effects of year of study, sex, and dominance rank were controlled for through partial correlation techniques. Conversely, the correlation between dominance rank and tail angles was not substantially improved by controlling for the effects of year of study, sex, and minimum estimated age. Finally, it should be noted

Table II. Relationship between dominance rank and tail position in adult male and adult female baboons

	r	r^2	LS regression equation (angle on rank)	n
Individual within rank means				
Adult males				
Angle 1	−0.10	1.0	angle = −0.62 (rank) + 61.81	42
Angle 2	0.09	0.8	angle = 0.54 (rank) + 35.82	42
Angle 3	0.18	3.2	angle = 1.15 (rank) + 104.71	42
Prox. seg. length/ Dist. seg. length	−0.38*	14.4	ratio = −1.14* (rank) + 36.73	42
Adult females				
Angle 1	−0.32	10.2	angle = −1.31 (rank) + 65.45	21
Angle 2	0.29	8.4	angle = 1.12 (rank) + 34.06	21
Angle 3	0.27	7.3	angle = 1.04 (rank) + 109.19	21
Prox. seg. length/ Dist. seg. length	−0.43*	18.5	ratio = −0.57* (rank) + 34.20	21
Raw data				
Adult males				
Angle 1	−0.30*	9.0	angle = −1.99* (rank) + 69.17	170
Angle 2	0.35*	12.3	angle = 2.12* (rank) + 27.95	170
Angle 3	0.38*	14.4	angle = 2.70* (rank) + 96.86	170
Prox. seg. length/ Dist. seg. length	−0.35*	12.3	ratio = −1.08* (rank) + 35.98	170
Adult females				
Angle 1	−0.25*	6.3	angle = −1.18* (rank) + 63.26	235
Angle 2	0.26*	6.8	angle = 1.25* (rank) + 34.03	235
Angle 3	0.18*	3.2	angle = 0.84* (rank) + 111.80	235
Prox. seg. length/ Dist. seg. length	−0.21*	4.4	ratio = −0.41* (rank) + 32.42	235

The table gives the Pearson product-moment correlation coefficient, coefficient of determination (r^2) and LS regression equation for each variable examined, including analyses based on individual within-rank means and on the raw data.

* Indicates a correlation coefficient or LS regression line slope that was statistically significant at 0.05 level.

Table III. Relationship between estimated minimum age and tail position in male and female baboons

	r	r^2	LS regression equation (angle on age)	n
Individual within census class means				
Males				
Angle 1	0.60*	36.0	angle = 3.65* (age) + 25.12	48
Angle 2	−0.73*	53.3	angle = −4.38* (age) + 78.31	48
Angle 3	−0.62*	38.4	angle = −4.05* (age) + 149.31	48
Prox. seg. length/ Dist. seg. length	0.28	7.8	ratio = 0.52 (age) + 24.13	48
Females				
Angle 1	0.70*	49.0	angle = 5.22* (age) + 22.10	35
Angle 2	−0.68*	46.2	angle = −5.83* (age) + 79.34	35
Angle 3	−0.73*	53.3	angle = −5.88* (age) + 154.89	35
Prox. seg. length/ Dist. seg. length	0.24	5.8	ratio = 0.76 (age) + 25.24	35
Raw data				
Males				
Angle 1	0.50*	25.0	angle = 3.30* (age) + 24.56	400
Angle 2	−0.53*	28.1	angle = −3.55* (age) + 75.23	400
Angle 3	−0.56*	31.4	angle = −3.95* (age) + 152.24	400
Prox. seg. length/ Dist. seg. length	0.27*	7.3	ratio = 0.75* (age) + 21.60	400
Females				
Angle 1	0.43*	18.5	angle = 4.72* (age) + 25.78	317
Angle 2	−0.47*	22.1	angle = −5.46* (age) + 76.51	317
Angle 3	−0.47*	22.1	angle = −5.68* (age) + 152.80	317
Prox. seg. length/ Dist. seg. length	0.17*	2.9	ratio = 0.77* (age) + 24.90	317

The table gives the Pearson product-moment correlation coefficient, coefficient of determination (r^2) and LS regression equation for each variable examined, including analyses based on individual within census class means and on the raw data.

* Indicates a correlation coefficient or LS regression line slope that was statistically significant at 0.05 level.

that both with respect to age effects and with respect to dominance rank effects, males and females showed very similar patterns of tail carriage changes.

An Age-Specific Tail Position?

Figure 7 shows scatter plots of angle 1 against age in months for the only two infants born in 1971 to survive through 1974; the birth date of both infants was known precisely and both infants were males. The least squares regression lines fitted to these data were calculated by excluding points obtained when the males were 6 months of age or younger. These graphs show a clear trend for increase in angle 1 with age after the first half year of life. The postneonatal correlation coefficient between angle 1 and age was 0.66 for Kub and 0.73 for Dogo, indicating that age accounted for 43.6 and 53.4%, respectively, of the variance in angle 1 for these two juveniles. The slope of the regression lines in figure 7 indicates that for each year of life after 6 months of age, the proximal portion of the tail was carried 14.3° closer to the vertical by Kub and 9.5° closer to the vertical by Dogo. Thus, it is likely that the slope of the regression lines shown in figures 5 and 6 would be increased substantially, were the birthdates of other members of Alto's group known precisely.

Based on the regression lines shown in figure 7, Kub and Dogo were expected to have carried the proximal segment of their tails no more than 1–2° above the horizontal from birth through 6 months of age. Instead, figure 7 shows that shortly after birth and throughout the first half year of life, these males carried their proximal tail segments from 30 to 70° above the horizontal (open circles, figure 7), though tail angles fell close to the expected in the second half year of life. Thus, a relatively sudden lowering of the proximal portion of the tail accompanied marked changes in fur and skin coloration during maturation into the infant-2 class (table I). It is possible that this higher than expected tail carriage, specific to infant-1's, functions together with other distinctive features of their external morphology to release the kinds of protective and other nonaggressive behaviors given by adult and juvenile baboons to newborn infants of their species [DeVORE, 1963].

Changes in Relative Length of Tail Segments

The tails of two different baboons can be characterized by the same set of angular measurements and yet appear very different in morphology to the observer and presumably to other baboons as well. Thus, changes in tail segment shape or relative segment length must also be examined in relationship to dominance rank and age. Two variables were chosen to assess changes

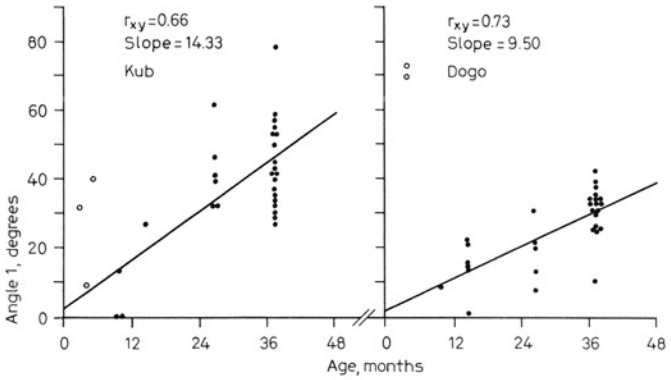

Fig. 7. Scatter diagrams and least squares regression lines of tail angle 1 (degrees) against true age (months) for two males of known birth date. Open circles indicate data points obtained while males were in the infant-1 census class; these points have been excluded in calculating the LS regression lines. See text for further explanation.

in the length of tail segments. The ratio of proximal to distal segment length measured differences in growth or elongation between the two portions of the tail. The point of projection of the tip of the tail onto the slightly flexed hindlimb measured changes in distal segment length relative to standing height. Obviously, these measures are affected not only by segment elongation, but also by the degree of curvature of the segments, by angles 1 and 2, and by differential growth of the hindlimb or body relative to the tail.

Figure 8 shows the proportion of photographs of individuals in each census class in which the tip of the tail projected onto the flexed hindlimb at a point below the middle of the tibia. In general, the tails of individuals in older census classes projected onto the hindlimb in a higher position than did the tails of individuals in younger census classes. For example, 57.1% (n = 7) of all photographs of infant-1's showed tail tip falling below midcalf, though only 1.7% (n = 405) of all photographs of adult showed a similar tail tip projection. The proportion of photographs with tail tips falling below midcalf declined steadily throughout the infant, juvenile and subadult classes. No systematic changes in tail tip projection were found in relationship to dominance rank, though in almost every census class a larger proportion of females than males had tail tips projecting below any given point, i.e. at most ages the distal tail segments of females were carried closer to the ground than the distal tail segments of males. In contrast, tables II and III show only a very weak correlation between the ratio of proximal to distal segment length and

either age or dominance rank in adults. Thus, apparently the relative lengths of the pre- and postjuncture segments of the tail are fixed early in life and, thereafter, show little change either as a result of rank changes or maturation.

Changes in Tail Shape

Figure 8 also shows the proportion of photographs of individuals in each census class that had a linear proximal segment, a linear distal segment, or an angular segment juncture. Photographs of individuals in the infant and juvenile classes most often had a linear rather than curved proximal segment. From the juvenile-2 class through the adult classes, however, the proportion of photographs with a linear proximal segment declined steadily from 99.2% (n = 119) of all photographs of juvenile-2's to 58.3% (n = 405) of all photographs of adults. Since no cases of a posteriorly curving proximal segment were recorded, figure 8 indicates that as individuals advanced in age the shape of their proximal tail segment frequently changed from linear to anteriorly curving. In contrast, the data on shape of distal segment showed that the proportion of photographs of individuals with linear distal segments was larger in the older census classes than in the younger census classes. Cases of both anteriorly and posteriorly curving distal segments were recorded. The proportion of photographs of individuals with an angular segment juncture increased from the infant-1 class through the juvenile-2 class and thereafter declined somewhat. No systematic changes in any of these categorical shape variables were found in relationship to dominance rank for either adults or younger individuals. In sum, age, not dominance rank, was the primary factor influencing tail position and shape in Amboseli baboons.

Discussion and Conclusions

This paper has shown that tail shape and position in Amboseli baboons changed regularly as a function of age. Among adults of both sexes there was no relationship between dominance rank and either tail position or shape, and the tail carriage of first-ranking males and females was neither characteristic or in any way distinguishable from that of lower ranking individuals. Although several authors have alluded to so-called dominant male tail positions among macaques, there has yet to be a systematic analysis of communication or status indication through tail position in a single primate species. Moreover, the few photographs or line drawings that have accompanied previous work on tail carriage do not constitute an adequate substitute

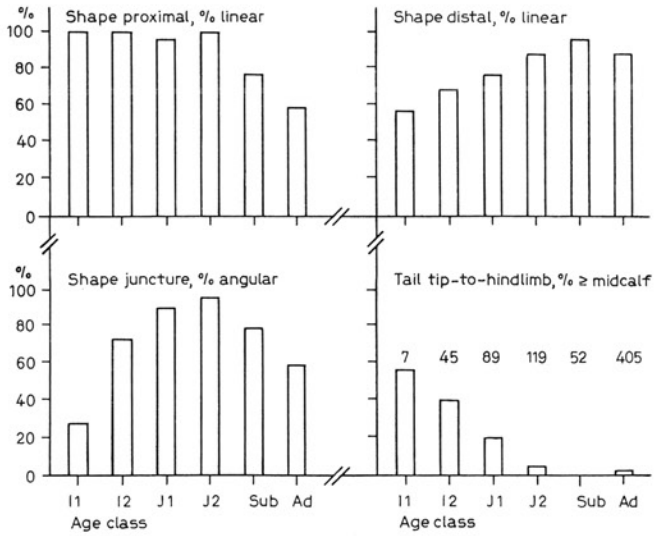

Fig. 8. Analyses of categorical tail shape variables. Figure shows proportion of all photographs that showed a linear proximal tail segment, linear distal tail segment, angular tail juncture or a tail tip-to-hindlimb projection falling at or below the middle of the tibia. Numbers over bars in lower right histogram indicate sample size of photographs used in all four analyses. See text for further explanation.

for quantitative data on the tail carriage of identifiable individuals of known age and dominance rank. Although this paper has demonstrated that age is one of the primary factors influencing neutral tail position in baboons, a much larger sample of photographs or filmed sequences of behavior will be required before the communicative function of the tail during social interaction can be analyzed in detail.

Anatomical Basis of Tail Carriage Changes

Although a complete developmental sequence of baboon skeletal material was not available, examination of specimens at the American Museum of Natural History suggests that specific osteological and myological changes underlie age-related changes in baboon tail carriage. In particular, the angle of the articular surfaces with respect to the long axis of the caudal vertebrae apparently changes during ontogeny. In young specimens the articular surfaces were nearly perpendicular to the long axis of the vertebrae; in older individuals the angle was much more oblique. The result of these morphological changes was to produce dorsal and anterior curvature of the first five or six caudal

vertebrae when articulated, or in other words to increase angle 1 and produce anterior curvature of the proximal segment of the tail. The extent of these changes differed between various baboon species apparently depending on the adult tail carriage. Thus, age-related changes in baboon tail carriage probably do not serve to signal changing social status with age, but merely reflect basic internal morphological changes. Presumably, the adaptive significance of these ontogenetic changes in tail carriage and morphology lies in the achievement of a specific adult tail carriage that, for example, may aid in species recognition or have some related function.

Finally, it should be pointed out that these morphological and behavioral changes in baboon tail carriage may provide an important system for further research and experimentation. Specifically, studies of the baboon tail allow exploration of the interface, or relationship, between morphology and behavior both within a developmental and an evolutionary perspective, and increasingly many of the most interesting and important research questions about primates concern this interface.

Summary

Tail position and shape was measured in 717 photographs of 54 individually identifiable yellow baboons *(Papio cynocephalus)* living in the Amboseli National Park, Kenya. Analyses of these data revealed that age was the primary factor influencing the neutral tail carriage of Amboseli baboons. The proximal segment of the tail was carried increasingly close to the vertical with increasing age; tail segment curvature also changed regularly in relationship to age. No relationship was found between dominance rank and neutral tail carriage for adult males or adult females, nor did first-ranking individuals have a tail carriage that was either distinctive or characteristic. The morphological basis of ontogenetic changes in tail carriage in baboons was also discussed.

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