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RESEARCH ARTICLES

Immigration and Hybridization Patterns of Yellow and Anubis Baboons In and Around Amboseli, Kenya

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In 1986, Samuels and Altmann reported evidence for a hybrid zone between *Papio anubis* and *Papio cynocephalus* in Amboseli, Kenya, in a baboon population that has been the subject of long-term study since 1971 [Samuels & Altmann, International Journal of Primatology 7:131–138, 1986]. In the current report we document ongoing patterns of hybridization in Amboseli between anubis and yellow baboons. In July 2000, we exhaustively scored living members of study groups for their degree of hybridity, using seven phenotypic characteristics (five in juveniles). We also scored all former members of study groups on the basis of photographic records, field notes, and observer recollections. A total of five anubis males and 11 males with hybrid phenotypes have immigrated into study groups over the course of the long-term study, and immigrations by hybrid males have increased in frequency over time. Further, the increasing frequency of hybrid phenotypes among animals born into study groups indicates that anubis and hybrid males have successfully reproduced in study groups. However, hybrid phenotypes and anubis immigrations were limited to groups in the southwestern portion of the Amboseli basin, with no hybrids occurring in the six eastern groups. Finally, we present evidence that anubis and hybrid males in Amboseli exhibit patterns of natal dispersal that are different from those of yellow males in Amboseli: males with anubis or hybrid phenotypes were significantly more likely to immigrate as juveniles or young subadults than were yellow males. Am. J. Primatol. 53:139–154, 2001.   © 2001 Wiley-Liss, Inc.

Key words: hybrids; hybrid zone; primates; dispersal

INTRODUCTION

In 1967, Maples and McKern reported a survey of baboons in Kenya, which indicated that the distributions of yellow and anubis baboons in the region around

Amboseli was defined by a 45-km gap of arid land in which no baboons occurred. On the eastern side of the gap (in what was then the Amboseli Game Reserve, later Amboseli National Park and environs) they found yellow baboons, and on the western side they found anubis baboons. The distributional gap narrowed as they moved north, and eventually the distributions of the two species joined in a hybrid zone northeast of Amboseli and southeast of Sultan Hamud, in the vicinity of Simba [Maples & McKern, 1967] (Fig. 1).

Maples and McKern [1967] did not survey the southern portion of the distributional gap, but our work has indicated that this gap closes in another hybrid zone immediately south and west of Amboseli National Park [Samuels & Altmann,
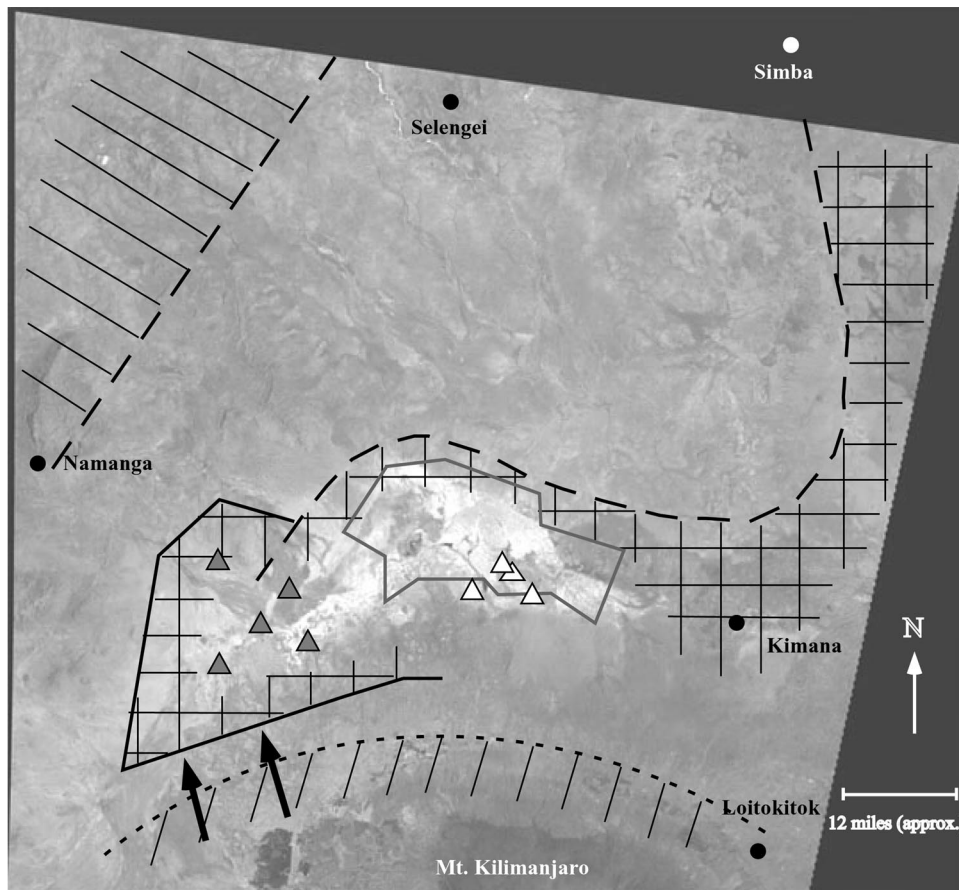

Fig. 1. Map showing the distribution of yellow baboons (cross-hatched lines) and anubis baboons (parallel lines) in the vicinity of Amboseli. The region shown here includes the southern part of the distributional gap described by Maples and McKern [1967]. They surveyed only in Kenya, and their range map stopped at the Kenya-Tanzania border (a straight line running between Namanga and Loitokitok). The additional range of yellow baboons reported in this work is shown with a solid black border. Anubis baboons are known to occur in the foothills of Kilimanjaro, but their range is not well defined (dotted line) [see also Samuels & Altmann, 1986]. Black arrows show the putative source of the anubis baboons that have immigrated into Amboseli. Gray borders show Amboseli National Park. Gray triangles represent hybrid study groups; an additional four nonstudy groups in their vicinity are hybrid. White triangles represent groups of yellow baboons with no hybrid or anubis members; two of these are former study groups and two are frequently-sighted nonstudy groups. Two additional all-yellow groups are known to occur near the eastern border of Amboseli National Park. All locations are approximate.

1986]. In particular, Samuels and Altmann [1986] reported on the immigration of a small mixed-sex group of anubis baboons into the southwestern part of the Amboseli basin in the early 1980s, and the immigration of two anubis males into a social group of yellow baboons [Samuels & Altmann, 1986]. In addition, they noted evidence that anubis baboons had probably entered the Amboseli population in the past. Samuels and Altmann [1986] suggested three possible sources of the anubis baboons in the Amboseli basin: 1) the northern Simba-Kiboko hybrid zone reported in Maples and McKern [1967]; 2) the anubis population at Namanga, due west of Amboseli; or 3) the foothills of Kilimanjaro, via the seasonal Olmolog river basin that flows into the southwestern portion of the Amboseli basin. They suggested this third route as most likely, given that all initial sightings of anubis animals had occurred in the southwestern portion of the region.

Since 1986, anubis males have continued to immigrate into Amboseli study groups at a low rate, and a number of males with a hybrid anubis-yellow appearance have immigrated as well. In addition, animals with hybrid phenotypes have been born into study groups in recent years. In the current study we document the increasing frequency of hybrid animals in the study population over the course of the long-term study. We also compare patterns of immigration by anubis, hybrid, and yellow males, which suggest that the anubis and hybrid males in our study population may disperse at an earlier age than the yellow males.

Natural hybridization within the genus *Papio* has been documented between anubis and yellow baboons and between anubis and hamadryas baboons [Maples & McKern, 1967; Nagel, 1973; Samuels & Altmann, 1986; Phillips-Conroy & Jolly, 1986; Phillips-Conroy et al., 1991]. Further, persistent patterns of anubis-yellow hybridization in the distant past may have contributed to the bushier, coarser mane of the "Ibean" type of yellow baboon typical of eastern Kenya, including Amboseli [Jolly, 1993]. Such hybridization has been important in the ongoing debate about whether the different baboons should have species or subspecies status within the genus [Hayes et al., 1990; Jolly, 1993]. Jolly [1993] proposed that the genus *Papio* be designated as monospecific, with nine subspecies. Although this approach is sound, we retain the species-level designations of *Papio cynocephalus* and *Papio anubis* for two reasons. First, these species-level designations are still in widespread use in spite of debate about nomenclature [e.g., Kingdon, 1997], and a monospecific nomenclature has not been widely applied in the literature. Second, it provides consistency with our previous publications [e.g., Altmann & Altmann, 1970; Samuels & Altmann, 1986]. However, we recognize that the taxonomy of the genus *Papio* is unsettled [Jolly, 1993].

METHODS

The baboon population in Amboseli has been the subject of ongoing demographic and behavioral research since 1971. Each of the study groups is monitored several days per week. All animals in study groups are recognized individually based on facial features, coat color, and other individual characteristics, and are well habituated to the presence of observers. Observers record all demographic events in study groups, including births, deaths, emigrations, and immigrations, as well as mating behavior, grooming, and a number of other behavioral and ecological data [e.g., Muruthi et al., 1991; Alberts & Altmann, 1995a, b; Altmann et al., 1996].

Phenotypes of Group Residents in July 2000

Our phenotype scoring method was based loosely on the methods of Nagel [1973] and Phillips-Conroy and colleagues [Phillips-Conroy & Jolly, 1986; Phillips-Conroy

et al., 1991] for hamadryas-anubis hybrids in Ethiopia. In scoring hybrid phenotypes in their population, Phillips-Conroy and colleagues [1991] focused on adult males, because the secondary sexual characteristics of hamadryas and anubis males are strikingly different and make for very clear, conspicuous hybrid characteristics. In contrast, we found that anubis-yellow hybrid characteristics were expressed in a very similar manner in adults and juveniles of both sexes. Consequently, we scored all animals (102 adults and 78 juveniles) in our five study groups (excluding infants under 1 yr) for their degree of hybridity. We excluded infants under the age of 1 yr because traces of the black natal coat remain through much of the first year in both species, and infants of the two species are similar in many other physical characteristics as well. Our definitions of what constituted yellow and anubis characteristics came from personal observations of yellow and anubis animals, as well as from published descriptions and illustrations of typical yellow and anubis phenotypes [Hill, 1970; Kingdon, 1974; Jolly, 1993; Kingdon, 1997]. As noted by Phillips-Conroy and colleagues [1991], a hybrid score of this kind reflects an animal's overall physical appearance, but does not provide direct genealogical information.

We used seven phenotypic characteristics, and scored each animal on each characteristic according to whether it showed a typical yellow phenotype for that characteristic (a score of 0), a typical anubis phenotype (a score of 2), or something in between (0.5, 1.0, or 1.5). Table I and Fig. 2 describe and illustrate the characteristics we used. The scores for the seven characteristics were then averaged to obtain a mean score. Four observers (S.C.A. and three field assistants) scored each animal, resulting in four mean scores for each animal. We then took the average of these four mean scores as the final phenotype score for the animal in question. We also calculated the standard deviations of these final phenotype scores to examine interobserver agreement. The mean standard deviation was 0.06, and the range was 0 (in the cases of animals for which all observers gave seven scores of 0, or pure yellow) to 0.31. Interobserver agreement on hybrid scores was thus quite good.

Phenotypes of Former Group Residents

We also scored animals that had previously lived in one of the study groups (146 natal adults and subadults, 128 natal juveniles, and 103 immigrant males). We scored these animals simply as yellow (0), hybrid (1), or anubis (2), based on photographic evidence, field notes, and observer recollections. Observers in this case included both authors (observing since 1984 and 1971, respectively) and three field assistants (observing since 1980, 1989, and 1996). Although not all five observers covered the entire span of the long-term data, the large majority of the study period included at least two of the five. Further, immigrations of anubis or hybrid animals have generally been noteworthy events, and the development of hybrid phenotypes in growing juveniles has likewise always attracted the attention of observers. In addition, in every case in which more than one observer scored the animal (i.e., in most cases of animals that survived to or were born since 1980) there was agreement as to whether the score should be 0, 1, or 2. Thus, as with hybrid scores of living animals, interobserver agreement for scoring from photographs, field notes, and recollections was quite good. In the analyses herein, the "hybrid" category includes both former study animals scored retrospectively as 1, and living study animals with scores in the hybrid range shown in Fig. 3.

We excluded from this study a former study group known as Lodge Group, and its two fission products (Lodge Group fissioned into two groups in 1996). Lodge Group and its fission products were the subjects of research for over a decade [e.g., Muruthi et al., 1991; Alberts, 1999]. However, as of July 2000, no

TABLE I. Phenotypic Characteristics Used for Hybrid Scoring

| Score	Pure yellow 0	More yellow 0.5	Intermediate 1.0	More anubis 1.5	Pure anubis 2
Coat color	Yellowish-brown, with lighter cheeks and belly		Dark brown with some yellow yellow highlights; cheeks and belly show some lightening		Olive brown, sometimes gray/black; cheeks and belly same color or with very slight lightening
Body shape	Appearing taller and thinner (see illustrations)		Intermediate		Appearing shorter and stockier with deeper chest (see illustrations)
Hair length	Relatively short, smooth and close to body but sometimes shaggy		Intermediate		Relatively long and coarse; in males, anubis mane stands out from head and body more than yellow mane (see illustrations)
Head shape	Top of the head pointed when viewed from the front, sometimes with a crest; in profile, forehead is not parallel with the angle of the muzzle (see illustrations)		Intermediate		Top of head not pointed when viewed from front; in profile, forehead is parallel with the angle of the muzzle (see illustrations)
Tail length and thickness	Longer (at least to back of knee) and thinner (see illustration)		Intermediate		Shorter (often above the knee) and thicker (see illustration)
Tail bend	Sharper "broken" appearance, with proximal part sometimes bent over the back (see illustrations)		Intermediate		Proximal part not curved over the back; generally a more arched appearance but variable, can appear bent (see illustrations)
Muzzle skin	White fur patches occur on the muzzle		Fur present on muzzle, but short and sparse		Skin is smooth and shiny with no fur present

A.

B.

C.
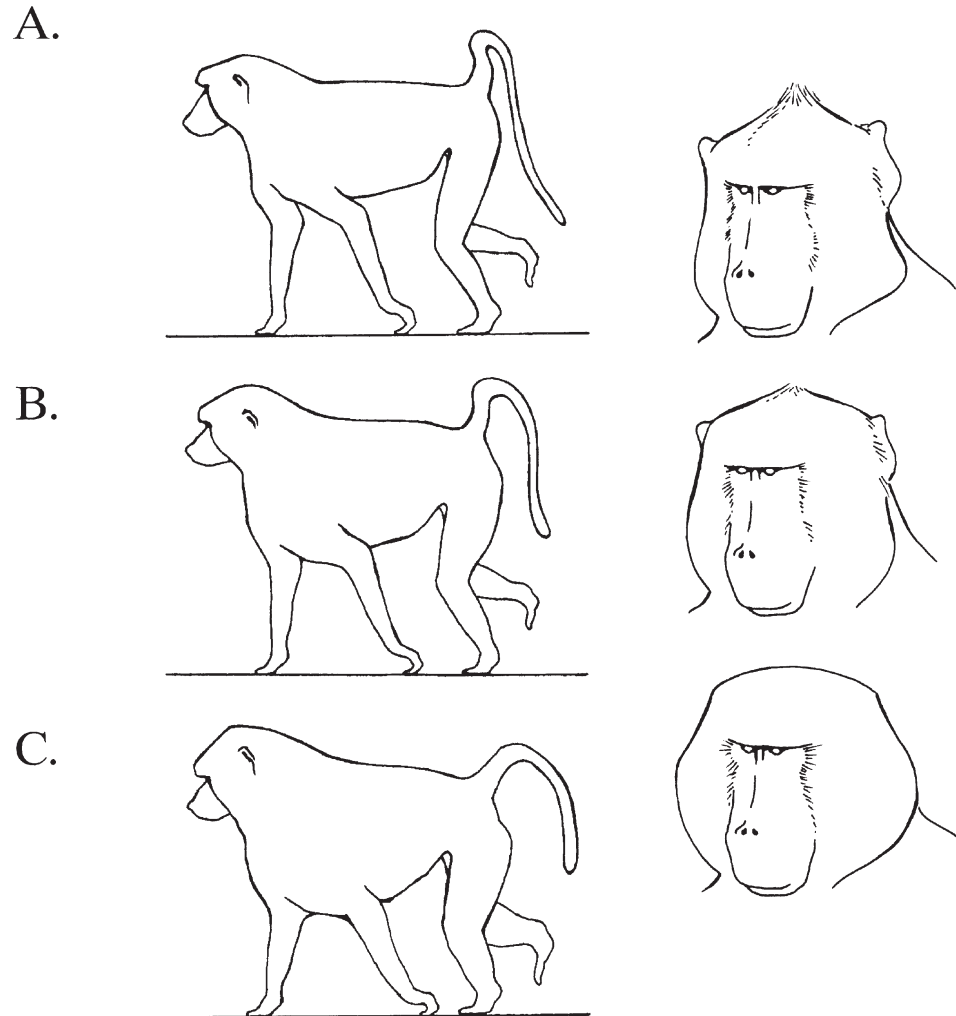
Fig. 2. Illustrations of key characteristics of (**A**) yellow, (**B**) hybrid, and (**C**) anubis baboons in Amboseli, in both profile and frontal views. Characteristics to note (see Table I) include: 1) the angle of the forehead relative to the muzzle (in profile), a feature due to differences in hair growth rather than skull anatomy; 2) shape of the top of the head (frontal view), again due to differences in hair growth; 3) the relative length and thickness of tails; 4) the tail bend; and 5) the body shape, apparently shorter and stockier in the anubis, with a deeper chest.

anubis or hybrid animals had been seen in these groups, which live approximately 20 km east of the five study groups that were the subjects of this study [Samuels & Altmann, 1991] (Fig. 1).

RESULTS
Phenotypes of Group Residents in July 2000

Final phenotype scores of living animals ranged from 0 to 1.89 (Fig. 3). Animals with scores of 0.25 and below were considered to be yellow baboons, based on overall physical appearance. These animals constituted 77% of animals in the
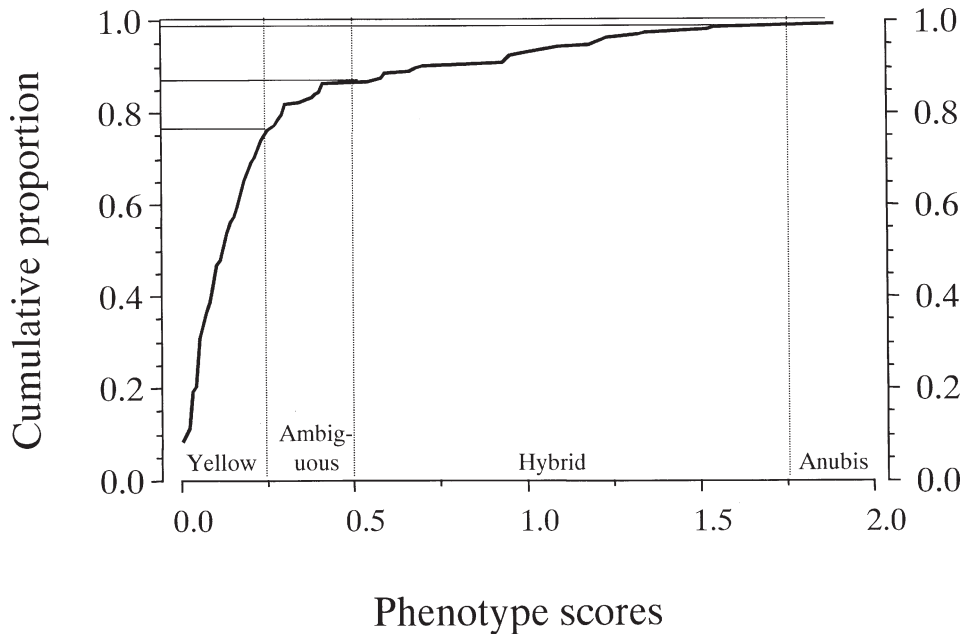
Fig. 3. Cumulative frequency distribution of phenotype scores for current members of study groups. The Y-axis indicates the proportion of animals in study groups that fell into a given phenotype category, shown along the X-axis. In July 2000, the study groups comprised 77% yellow baboons (scores of 0–0.25), 10% ambiguous phenotypes (0.26–0.49), 13% hybrid phenotypes (0.50–1.54), and only a single anubis male.

five study groups (Fig. 3 and Table II). The single anubis male living in a study group in July 2000 had a final phenotype score of 1.89. We defined confirmed hybrids as those with scores ranging from 0.50 to 1.54 (there were no individuals with scores between 1.54 and 1.89). Hybrids constituted 13% of animals in the five study groups. The remaining 18 animals (10% of the study animals; Fig. 3 and Table II) had ambiguous phenotypes, with scores ranging from 0.26 to 0.49. In some cases these were likely to have been hybrids with one anubis grandparent. In other cases they may have had a more distant anubis ancestor, or may simply have been an outlier on the spectrum of yellow phenotypes. Yellow baboons are defined by three subtypes (Kinda, Ibean, and Typical) that exhibit a range of body size, coat color, and hair thickness [Jolly, 1993; Hill, 1970]. The yellow baboons in Amboseli most resemble the Ibean subtype, but Amboseli is near the geographic distribution of the Typical subtype [Jolly, 1993], and like all natural populations it exhibits a range of phenotypes.

Phenotypes of Former Group Residents

Among natal animals that died or disappeared as adults, subadults or juveniles over 1 yr of age, seven of 279 were deemed hybrid based on photographic records and observer recollections (see Methods). One, a female, had an estimated birth date of 1969 (two years before observations began). A second, her son, was born in 1975 before any immigrations by anubis males were recorded. These two animals were unusually dark and stocky, and examination of photographs suggested that in both cases a classification of hybrid was warranted, although the male born in 1975 could not have been more than one-quarter anubis.

TABLE II. Phenotypes of Current Group Residents, July 2000

	Yellow baboons (0–0.25)	Ambiguous phenotypes (0.26–0.49)	Hybrid baboons (0.50–1.54)	Anubis baboons (>1.75)
Immigrant males	17	9	10	1
Natal adults	54	4	8	0
Natal juveniles	67	5	5	0

The remaining natal hybrids were all born after the first documented immigrations of anubis males into study groups. Twenty-eight dead juveniles could not be ruled out as hybrids because photographs and observer recollections were lacking in these cases. Among the 110 immigrant males that are no longer in the population two were hybrid, four were anubis, and three could not be assigned a phenotype due to lack of photographic evidence and observer recollections (Table III).

Changes Over Time

On average, anubis males immigrated into study groups once every 3.5 years beginning in 1982 (years of immigration for the five anubis, four of which were
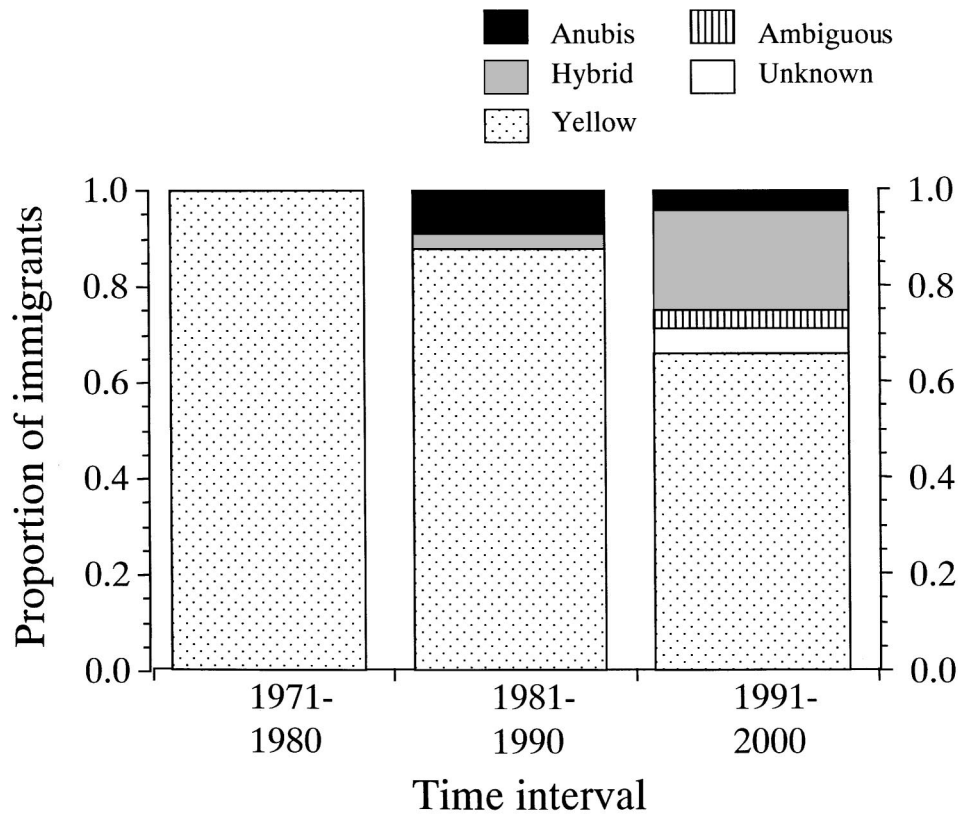

Fig. 4. Immigrants into study groups by decade. Proportion of anubis and hybrid immigrants has increased over time.
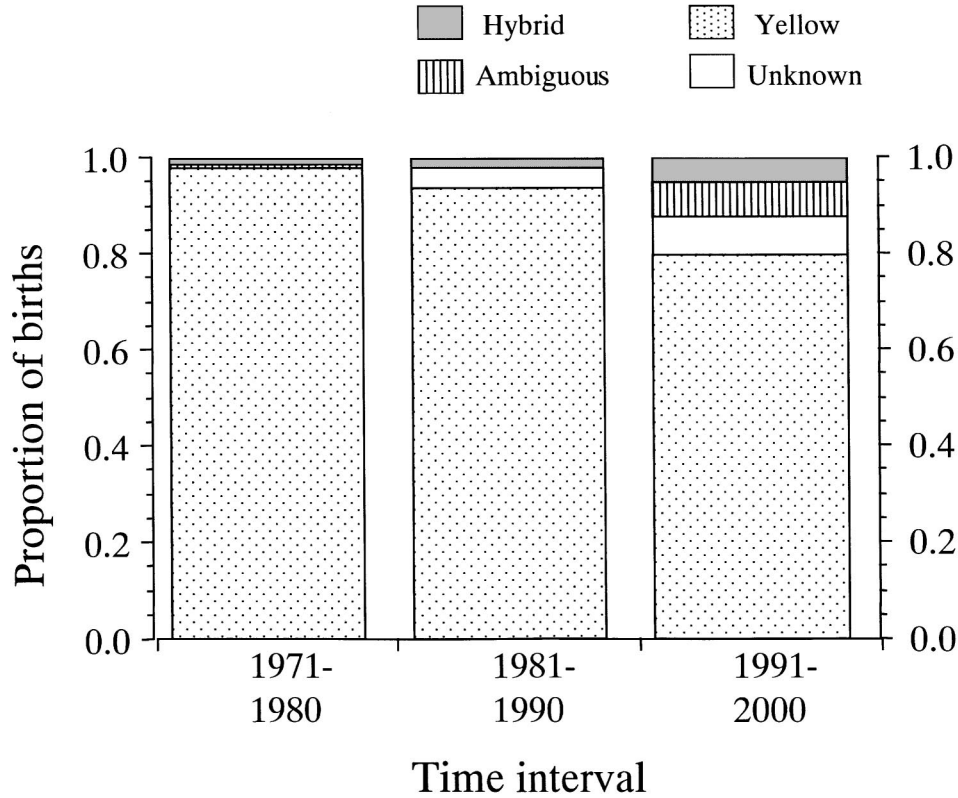
Fig. 5.   Births in study groups by decade. Proportion of hybrid births has increased over time.

no longer in the population as of July 2000, were 1982, 1984, 1987, 1992, 1996). In contrast to this low and fairly steady rate of anubis immigration since the 1980s, the proportion of immigrants that expressed hybrid or ambiguous phenotypes increased substantially, from 0 in the 1970s to 3% in the 1980s and nearly 25% in the 1990s (Fig. 4). The proportion of hybrid births and births of ambiguous phenotypes tells a similar story. Even before any immigrations by anubis males, a very small number of animals with a hybrid or ambiguous appearance occurred (Fig. 5), probably reflecting introgression of anubis genes into the yellow population in the past. However, beginning in the 1980s, the number of hybrid and ambiguous phenotypes among animals born into study groups increased substantially (Fig. 5).

   This increase in the number of hybrids but not of anubis animals reflects the successful reproduction of anubis males in groups of yellow baboons, as well as the successful reproduction of yellow males in the single anubis group that immigrated into the basin (see Introduction). When first seen, this group included two yellow males, two anubis males, and four anubis females with juveniles (i.e., there were no hybrids among adults) [Samuels & Altmann, 1986]. Over the years, this group has increasingly come to consist of animals with a hybrid appearance, and relatively few animals with a pure anubis phenotype persist (unpublished data from opportunistic sightings; this group is not a study group). The fact that young, fully anubis males continue to immigrate into study groups from time to time
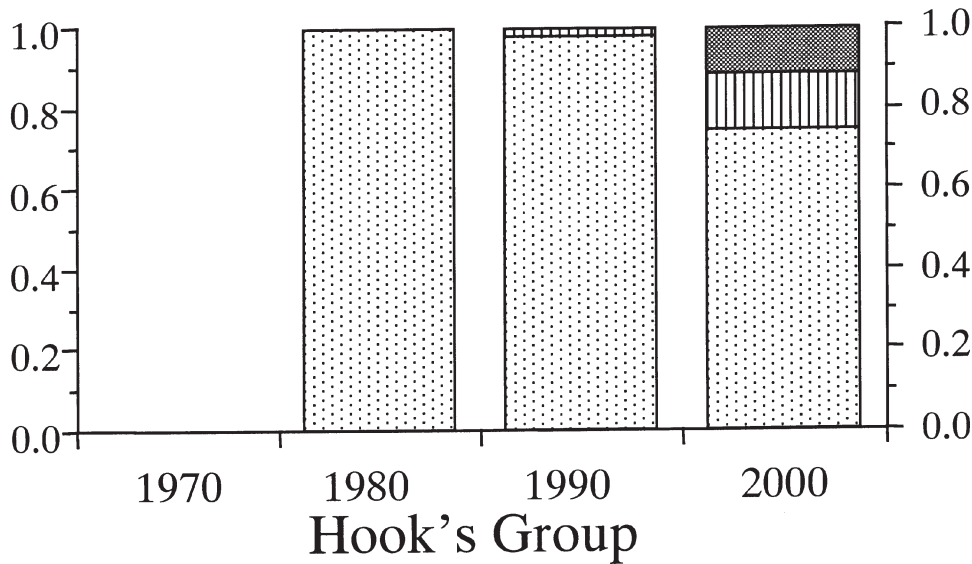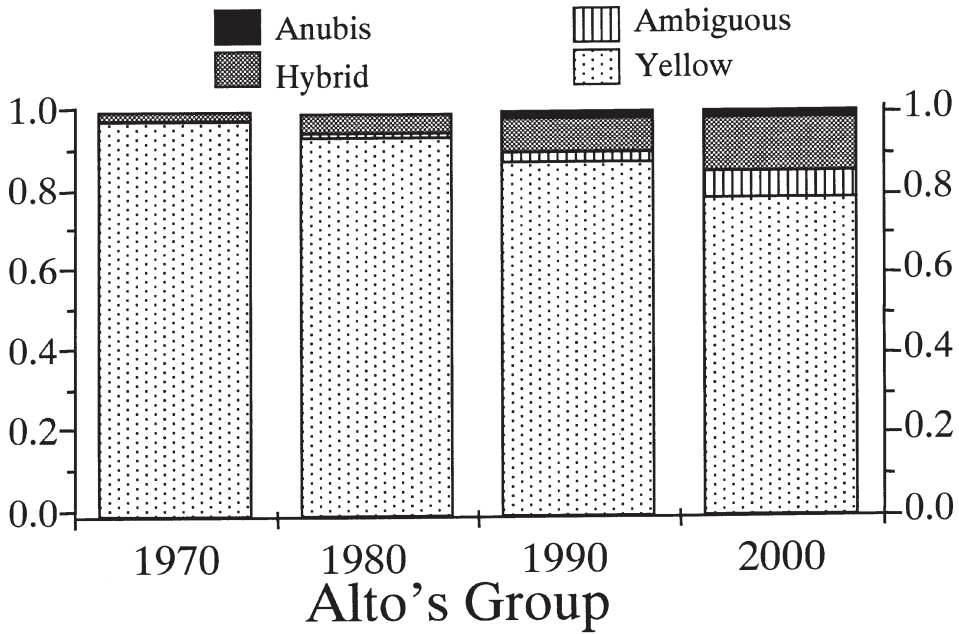
Fig. 6. Proportion of anubis or hybrid members of study groups has increased over time. Each bar represents a census taken on July 1 of the year indicated; censuses with individual identification were not available for Hook's Group in 1970. Note that Alto's Group, which ranged further south and west than Hook's Group, developed a pattern of hybridization earlier than Hook's Group (see text).

suggests that this group has not been the only source of anubis baboons, but that lone males occasionally immigrate into the Amboseli basin, most likely from the foothills of Mt. Kilimanjaro [Samuels & Altmann, 1986] (see Introduction).

Geographical Patterns of Hybridization

Alto's Group was the first of the study groups to receive anubis immigrants [Samuels & Altmann, 1986], probably because it ranged considerably further west of the other study groups through the 1980s [Samuels & Altmann, 1991]. In 1987 Alto's Group shifted its range 5 km further west and 5 km south [Bronikowski & Altmann, 1996], bringing it closer to the probable source of anubis animals, the foothills of Kilimanjaro [Samuels & Altmann, 1986] (see Introduction). By 1990, Alto's Group and its fission products (the group fissioned into three groups between 1989 and 1991) consisted of nearly 10% anubis and hybrid animals (Fig. 6). In contrast, Hook's Group remained an entirely yellow group through the 1980s. It was not until 1992, a year after Hook's Group shifted its range 6 km west (into the same region as Alto's Group had previously moved [Bronikowski & Altmann, 1996]), that it received its first anubis immigrant. Consequently, it was not until the end of the 1990s that Hook's Group and its fission products (the group fissioned into two groups in 1994) approached the same proportion of hybrid animals as Alto's Group and its fission products (Fig. 6).

Immigration Age

In Amboseli, the large majority of males immigrate as adults; that is, they are at or near their full size, and they immediately begin challenging other adult males in agonistic encounters and consorting with adult females. Juveniles (males that have not yet achieved testicular enlargement [Alberts & Altmann, 1995a]) and subadults (pubescent males that are still undergoing the adolescent growth spurt and have not yet successfully challenged adult males in agonistic encounters [Alberts & Altmann, 1995a]) are rare among immigrants. When juveniles or subadults immigrate, they behave very much like resident juvenile and subadult males, and may wait several years in the new group before growing large enough to challenge adult males in physical contests or consort with adult females.

We observed that a large proportion of the males that immigrated into study groups as juveniles or subadults were anubis or hybrid (Tables IV and V). We compared numbers of hybrid or anubis immigrants with yellow immigrants in each age group using a G test with a Williams correction [Sokal & Rohlf, 1995] and found that anubis and hybrid phenotypes were significantly overrepresented among juvenile and subadult immigrants (Table IV; G_{adj} = 9.59, $P < 0.005$). It should be noted that three of the hybrid immigrants in this analysis (two subadults and one adult) were hybrid males born into study groups. Therefore, they appear as natal animals in Tables II and III, but because they successfully immigrated into other study groups they also appear in this analysis of age at immi-

TABLE III. Phenotypes of Former Group Residents

	Yellow baboons	Hybrid baboons	Anubis baboons	Unknown phenotypes
Immigrant males	95	2	4	3
Natal animals	244	7	0	28

TABLE IV. Males With Anubis or Hybrid Phenotypes Were Over-Represented Among Males That Immigrated Before Adulthood*

	Number that immigrated as juveniles or subadults	Number that immigrated as adults	Percent that immigrated as juveniles or subadults
Yellow phenotypes	3	114	2.6%
Anubis or hybrid phenotypes	5	14	35.7%

*$G_{adj} = 9.59$, $P < 0.005$.

gration; this is true of a number of yellow males as well. One juvenile immigrant male was excluded from this analysis. He entered a study group in his infancy, at the estimated age of 10 months, and remained there for 53 days before disappearing. He was the youngest immigrant ever recorded in Amboseli (the next youngest was estimated to be 3.5 years old at immigration (Table V)). His phenotype was unknown; photographs taken during his residency in the study group reveal a very thin infant with a dark coat that had a bedraggled appearance and may have had remaining traces of the black natal coloration typical of both yellow and anubis infants. If we include him as a yellow baboon in this analysis, the difference between phenotypes is still significant ($G_{adj} = 8.43$, $P < 0.005$).

This pattern would be produced if anubis and hybrid males experienced relatively poor social integration in the groups from which they emigrated, or if they were more vulnerable to early eviction than yellow males. However, as several authors have noted [see Pusey & Packer, 1987, for review; Packer, 1979, for anubis baboons], dispersal in baboons and many other cercopithecines rarely involves eviction or even increased aggression from residents. Similarly, in our study dispersals that could be characterized as evictions (i.e., preceded by intense aggression directed towards the eventual emigrant) were extremely rare. None have ever involved hybrid or anubis males, and in particular the hybrid males that emigrated from study groups as subadults (Table V) dispersed with no evidence of eviction. Further, in the study groups, anubis and hybrid males engage in agonistic interactions and mate guarding in a manner similar to that of yellow males. Samuels and Altmann [1986] documented the rapid social integration of the anubis immigrant they observed, and our subsequent observations of both anubis and hybrid immigrants have supported this observation. There appears to be no discrimination against these males on the part of females, nor are they behaviorally unusual among their yellow male peers. Lack of discrimination in the groups they enter suggests a lack of discrimination in the groups from which they departed.

DISCUSSION

As of July 2000, hybrid baboons in Amboseli were restricted to the southwestern part of the Amboseli basin, where all five study groups as well as four nonstudy groups contain hybrid animals [Samuels & Altmann, 1991] (Fig. 1, and unpublished data). The six more eastern groups [Samuels & Altmann, 1991], including the two fission products of Lodge Group, contained no hybrid animals, and no anubis males had immigrated into these groups as of July 2000.

Samuels and Altmann [1986] suggested that the most likely source of anubis immigrants in Amboseli was the forested slope of Kilimanjaro. Their proposed entrance route was the seasonal Olmolog river basin, which flows into the southwestern portion of the Amboseli basin. Since that study, anubis immigrants have

TABLE V. Males That Immigrated Into Study Groups Before Reaching Adulthood, Amboseli, 1971–2000*

Name	Immigration group	Source group	Immigration date	Known (*) or estimated (**) age at immigration (years)	Status at entry	Phenotype
Nog	Alto	Unknown	19 May 1974	3.5**	Juvenile (entered before TE)	Yellow
Janubis	Hook	Unknown	20 Jan. 1992	4.0**	Juvenile (entered before TE)	Hybrid
Giza	Alto	Unknown	11 Feb. 1984	4.5**	Juvenile (entered before TE)	Anubis
Exodus	Nyayo (Alto fission product)	Unknown	21 Jan. 1995	5.0**	Juvenile (entered before TE)	Yellow
Orlon	Hook	Dotty (Alto fission product)	04 Apr. 1994	5.6*	Young subadult (entered at or near TE)	Hybrid
Ruto	Hook	Stud	02 Nov. 1986	6.5**	Subadult (entered after TE but 19 mo before rank attainment)	Yellow
Alex	Hook	Unknown	04 Mar. 1994	7.0**	Young subadult (entered at or near TE)	Hybrid
Oryx	Weaver (Hook fission product)	Dotty (Alto fission product)	11 Apr. 1997	7.1*	Subadult (entered after TE but 6 mo before rank attainment)	Hybrid

*"Entered before TE" means that the male immigrated before he had reached testicular enlargement, the development marker that signals the onset of subadulthood (see text). Males are listed in order of age at immigration (from young to oldest).

continued to appear initially in the southwestern part of the basin, and only groups with southwestern ranges had received anubis immigrants by July 2000. Further, the anubis population on Kilimanjaro is the closest anubis population to Amboseli (Fig. 1). Hence, our observations support the view that the Kilimanjaro population is the probable source of anubis animals into Amboseli.

The increase in the number of hybrid animals in Amboseli after 1982 suggests that this baboon hybrid zone is undergoing a change in structure. If the low but steady rate of anubis immigrants into Amboseli continues, then hybridization is likely to continue to increase, as hybrid animals survive and reproduce well in groups of yellow baboons. Mt. Kilimanjaro is increasingly under cultivation by a growing human population, and the resulting pressure on wildlife populations may be one cause of anubis immigrations in the 1980s and 1990s. If so, anubis immigrations into Amboseli might be expected to increase and even spread throughout the basin, with a concomitant increase in the hybrid population. Eventually, however, the Kilimanjaro anubis population may be reduced or eliminated due to inevitable conflicts between baboons and humans, and anubis immigrations into Amboseli may cease or become very rare. If this occurs, the Amboseli population will presumably return to the condition it exhibited in the 1970s, when the large majority of phenotypes were yellow but hybrid and ambiguous phenotypes occasionally occurred. As noted, such periodic contact and hybridization between anubis and yellow populations have almost certainly occurred repeatedly during the species' evolutionary history, and the *ibeanus* phenotype common in Kenya, with a coarser, thicker mane than the typical yellow phenotype further south, may reflect this historical pattern of hybridization [Jolly, 1993].

The other well-described baboon hybrid zone, in the Awash National Park in Ethiopia, has also undergone structural changes over relatively short time periods [Phillips-Conroy & Jolly, 1986], apparently due to climatic fluctuations in the study area. In that study, the hybrid zone between anubis and hamadryas baboons is characterized by a more bimodal distribution of hybrid phenotypes. That is, hybrids in that study tend to be either anubis-like hybrids or hamadryas-like hybrids [Phillips-Conroy & Jolly, 1986; Phillips-Conroy et al., 1991]. In contrast, the distribution of phenotype scores in Amboseli showed a continuous distribution from scores of 0–1.5 (Fig. 3). This was true even if we only considered adult males, as did Phillips-Conroy and colleagues [Phillips-Conroy & Jolly, 1986; Phillips-Conroy et al., 1991].

Our immigration data suggest that anubis and hybrid baboons in Amboseli are more likely to disperse as juveniles or subadults than are yellow baboons. Among Amboseli yellow baboons, median age at dispersal is 8.5 years [Alberts & Altmann, 1995b], very close to the peak dispersal age reported for anubis baboons in Gombe, Tanzania [Packer, 1979; Packer et al., 1995]. However, 7% of anubis baboons in Gombe disperse by age 6, as juveniles or pubescents, and roughly 16% disperse by age 7 [Packer et al., 1995]. In contrast, among yellow baboons in Amboseli dispersal before the age of 7 is uncommon [Alberts & Altmann, 1995b], and only 2.6% of males immigrate into new groups as juveniles or subadults (Table IV).

Two hypotheses may be proposed to explain this difference (a third hypothesis, that hybrid animals are socially ostracized and evicted at a younger age, is not supported by our data). First, it is possible that the difference between anubis/hybrid and yellow baboons in Amboseli reflects a widespread difference between anubis and yellow baboons. The comparative data for Gombe and Amboseli support this hypothesis to some extent, although age at dispersal in Gombe does not appear to be as biased towards juveniles and subadults as the Amboseli data on

anubis and hybrids. A second hypothesis is that the anubis baboons in Amboseli represent a subset of the Kilimanjaro population with an unusually strong propensity for dispersal, which results both in their moving relatively long distances during dispersal, and doing so at a relatively young age. More extensive comparative data from studies of anubis and yellow baboons will help to distinguish these two hypotheses. A difficulty with collating comparative data will be site differences in how juvenile and subadult age classes are defined. We use unambiguous physiological and behavioral markers to define age classes in Amboseli [Alberts & Altmann, 1995a], and encourage others to do the same in order to facilitate intersite comparisons. In the absence of such markers, age may be a reasonable proxy. In our data set, wild-feeding males rarely attained testicular enlargement (reached subadulthood) before 5 years and rarely attained adult dominance rank (reached adulthood) before 7 years [Alberts & Altmann, 1995a]. However, males in the semi-provisioned Lodge Group grow more rapidly and reach all developmental markers earlier than males in the wild-feeding groups (Altmann and Alberts, unpublished data). Thus, developmental rates show considerable phenotypic plasticity, making intersite comparisons based on age less desirable than comparisons based on developmental markers.

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