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Immigration of a *Papio anubis* Male into a Group of *Papio cynocephalus* Baboons and Evidence for an *anubis–cynocephalus* Hybrid Zone in Amboseli, Kenya

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The 1982 observation of the immigration of an adult male olive baboon, Papio anubis, *into a group of yellow baboons,* Papio cynocephalus, *in Amboseli National Park, Kenya, constitutes the first confirmed report of interbreeding between the two species within the Amboseli baboon population. We document the social aspects of the immigration and describe subsequent sightings of* anubis *baboons in Amboseli that confirm the existence of a previously unrecognized hybrid zone in Kenya.*

KEY WORDS: hybrid zone; male transfer; *Papio anubis; Papio cynocephalus.*

INTRODUCTION

In December 1982 an adult male olive baboon, *Papio anubis,* immigrated into Alto's Group, a group of yellow baboons, *Papio cynocephalus,* in Amboseli National Park, Kenya. Although we have evidence to suggest that *anubis* baboons may have been in and out of the Amboseli ecosystem in the past, the present observations constitute the first

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confirmed report of gene flow between Amboseli *cynocephalus* and migrant *anubis* baboons since studies of the population began in the 1960s. In addition, this report documents the social aspects of the *anubis* male's entry into the *cynocephalus* group. Subsequent observations of other *anubis* baboons in the Amboseli basin establish the existence of a previously unrecognized *anubis-cynocephalus* hybrid zone in Kenya.

RECENT HISTORY OF *ANUBIS* BABOONS IN AMBOSELI

Prior to 1982, there was a single sighting of an *anubis* baboon in the Amboseli basin. On 29 January 1972, an adult male *anubis* was observed with a group of *cynocephalus* baboons in the southwestern portion of the basin (G. Hausfater, unpublished data). The *anubis* male had not been present when the group was censused 6 weeks earlier, nor was he present when the group was encountered again 1 month later.

Maples and McKern (1967) reported a sharp demarcation between the Amboseli *cynocephalus* baboons and the nearest Kenyan *anubis* baboons at Namanga. These two populations were separated by a dry lake bed, a gap of 45 km. Maples did not survey into Tanzania, south and west of Amboseli. However, *anubis* baboons have been seen on the lower northern slopes of Kilimanjaro as recently as 1977 (B. Oguya and D. Western, personal communications).

METHODS

Surveys. The baboons of the western portion of the Amboseli basin have been surveyed regularly since 1963 when the Altmanns initiated periodic censusing of that population (Altmann *et al.*, 1985). The following year Maples mapped the distribution of *anubis* and *cynocephalus* baboons in southern Kenya, from Nairobi to the Kenya-Tanzania border, including the Amboseli area (Maples and McKern, 1967). In November-December 1984, a census of the baboons of the entire Amboseli basin was conducted (Samuels *et al.*, 1986). In addition, the ongoing intensive study of the behavior and ecology of two of the Amboseli baboon groups (Alto's Group, studied since 1971; Hook's Group, since 1981) provided observation of frequent encounters with other baboon groups in the area.

Behavioral Data. Information on the social integration of the *anubis* male was derived from data collected for several ongoing projects. For the period December 1982 through June 1983, we used data gathered as part of

the longitudinal study of sexual, affiliative, and agonistic associations of Alto's Group members. All consortships, grooming bouts, and agonistic interactions [terms as defined by Hausfater (1975) and Hausfater *et al.* (1982)] of all group members were recorded on an *ad libitum* basis, and records of female reproductive state were made each morning (Altmann and Altmann, 1970). For the period January through March 1983, supplemental information was derived from systematic focal sampling of all adult females, in which the identity of adult males within 5 m of the focal female (referred to as her "neighbors") was recorded. We used these data sets to determine the dominance status of the new male and the identities of his affiliative associates, sexual partners, and likely offspring. We considered the new male to be a likely father (Altman *et al.*, 1986) of infants with whose mothers he consorted on the probable days of conception (Gillman and Gilbert, 1946; Hendrickx and Kraemer, 1969).

RESULTS

In November 1982 during the short rains (Altmann and Altmann, 1970), a mixed *anubis-cynocephalus* baboon group, the Ositeti Group, was first sighted in the southwestern portion of the Amboseli basin. This group consisted of 15 baboons: 4 adult males (2 *anubis*, 2 *cynocephalus*), 1 *cynocephalus* subadult male, 4 adult females (all *anubis*), and 6 juveniles. Sightings of this group were brief because these baboons were unhabituated to humans or to vehicles. Nonetheless, it was the impression of observers that several of the juveniles were yellow in coloration but had *anubis*-like features (e.g., stocky builds and *anubis*-shaped tails and faces). Ositeti Group baboons remained in the area through December and interacted with members of Alto's Group several times. During this time period, two adult males transferred from the Ositeti Group into Alto's Group—a *cynocephalus* male in November and an *anubis* male in December. We have seen the Ositeti Group in the basin since the initial sightings in 1982 but only in the southwestern portion and only during subsequent rainy periods: April 1983, December 1983, and November 1984 to January 1985.

Since the arrival of the Ositeti Group in the area, we have seen several other *anubis* baboons. In February 1984, a second *anubis* male, a juvenile male estimated to be 4.5 to 5 years old of unknown origin, joined Alto's Group. In November–December 1984, during a basin-wide survey of Amboseli baboons (Samuels *et al.*, 1986), we found another mixed *anubis-cynocephalus* group. As with the Ositeti Group, these baboons were seen only in the southwestern portion of the Amboseli basin, and as in Alto's Group, the only *anubis* members of the group were males.

Social Aspects of the Immigration

Darwin, the migrant *anubis* male from the Ositeti Group, transferred into Alto's Group on 18 December 1982, a day during which the two groups had several peaceable encounters. During these meetings, Darwin was observed to interact with a number of Alto's Group members, including the two highest-ranking adult males, adult females of all reproductive states, and juveniles. In the late afternoon when the two groups separated, Darwin traveled with Alto's Group to the sleeping trees and remained with Alto's Group thereafter.

On his day of entry into the group, Darwin was the "winner" [as defined by Hausfater (1975)] of at least one fight with the second-ranked male, but in subsequent interactions the second-ranked male was always dominant to Darwin. Due to the small number and anomalous outcomes of the agonistic interactions of Darwin with other males during his first few weeks, we were unable to assess his dominance status accurately until January, when he was sixth-ranked among 10 adult males. By February 1983 he dropped to the eighth rank of 11 males and remained in this rank until the end of the study period, June 1983.

During his first 6 months in Alto's Group, Darwin continued to have an unusually tense relationship with the second-ranked male. More than one-quarter (44/157 = 28%) of the second-ranked male's agonistic interactions were with Darwin, who was 1 of 10 other males in the group. In addition, these two males occasionally had agonistic interactions which neither male won.

Darwin's social integration into Alto's Group was rapid. Within 2 weeks of his entry he was sexually active and had formed associations with several adult females. These relationships persisted for the next 6 months. He formed consortships with 10 of the 14 females that were sexually cycling during this time period, January through June. He consorted with a mean number of 2.5 females per month (of a mean number of 6.8 cycling females available per month). He was a likely father of 5 of the 12 infants conceived during this period. Two of these infants were conceived in January, within 1 month of his immigration. Four of the five conceptions resulted in live births; only two of these infants survived the first year of life.

Darwin's most common associates during his first 6 months in Alto's Group were sexually cycling females and pregnant females with whom he had consorted. A disproportionate number of his grooming bouts (215/257 = 83.7%) were with cycling females (47.1%) or with pregnant females (35.9%) with whom he had consorted during their conception cycle. Half of his grooming bouts (129/257 = 49.8%) were with the five mothers of his likely offspring, both before and during pregnancy. This pattern of association was corroborated by the sampling of adult male neighbors of adult

females during January–March. Darwin was a neighbor in 32 samples; in 78%) of those samples, the focal female was a cycling female or a pregnant female with whom he had consorted during her conception cycle, compared to the 59% expected on the basis of the average percentage of females that were in this category per month. Three-quarters (19/25 = 76%) of these associations were with four of the mothers of his likely offspring.

In sum, Darwin's preferred associates, identified from both grooming and neighbor data sets, were three of the mothers of his likely offspring, a female with whom he consorted often but not during her conception cycle, and a female that cycled intermittently during January–June but did not conceive. Three of these females were sisters of the top-ranking matriline, one was another high-ranking female, and the fifth was an elderly female that dropped from the middle to the bottom of the female dominance hierarchy during this time period.

DISCUSSION

The migrant *anubis* male entered and was assimilated rapidly into Alto's Group. His mating success indicates an absence of the behavioral reproductive isolating mechanisms described for *P. anubis* males and *P. hamadryas* females (Kummer *et al.*, 1970; Nagel, 1973). However, the immigration of male baboons is not a well-studied phenomenon even when all participants are of the same species. We are therefore unable to assess to what extent the rapidity of entry and integration can be attributed to the immigration of an *anubis* male into a *cynocephalus* group rather than to the variability that exists among male baboons. The technique of entry of a particular male and the interval of time until he is able to establish sexual and affiliative associates seem to depend upon a combination of factors, including his age, his experience, his dominance rank, and his personality as well as qualities of the group he enters (e.g., Altmann and Altmann, 1970; Packer, 1979; Strum, 1982; van Noordwijk and van Schaik, 1985; Manzolillo, in press). Darwin's mating success, for example, might be attributed to the large number of adult females that were sexually cycling at the time of his entry.

The appearance of three mixed *anubis–cynocephalus* groups in the Amboseli basin since late 1982 establishes the existence of a new or unstable hybrid zone in Amboseli. Although we have no information concerning the period prior to the 1960s, Hausfater's 1972 sighting of an *anubis* and the presence of several dark-coated, but otherwise *cynocephalus*-featured, adult baboons in Amboseli suggest the possibility that *anubis* baboons may have inhabited the region in the past.

The compositions of the three mixed groups, the regions of their ranging, and the seasonality of the appearance of *anubis* indicate that the Ositeti

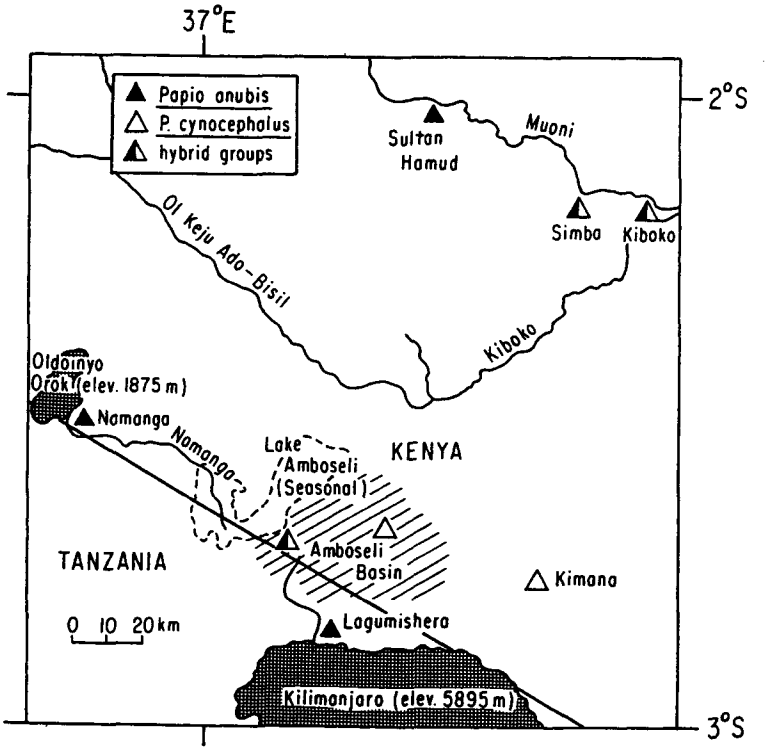

Fig. 1. Possible routes of migration of *P. anubis* baboons into the Amboseli basin (indicated by diagonal hatching) via the seasonal Kiboko, Namanga, or Olmolog rivers. Note that only selected topographical features are shown. Sightings of groups of *P. anubis* are represented by filled triangles [Lagumishera (Oguya and Western, personal communications); Namanga and Sultan Hamud (Maples and McKern, 1967)]. Open triangles denote reports of *P. cynocephalus* groups [Amboseli (Maples and McKern, 1967; Altmann and Altmann, 1970; this study); Kimana (van Citters *et al.*, 1967; Altmann and Altmann, 1970)]. The half-filled triangles represent observations of hybrid groups [Simba and Kiboko (Maples and McKern, 1967); Amboseli (this study)].

Group is likely to be the source of the *anubis* invasion into Amboseli. Because females are the sex that does not disperse, we know that Alto's Group and the other mixed group are *cynocephalus* groups into which *anubis* males have immigrated. Ositeti Group is an *anubis* group that has acquired some yellow males.

There are several possible routes of entry for *anubis* baboons into this *cynocephalus* population (Fig. 1). During the rains, baboons from the Simba–Kiboko hybrid zone (Maples and McKern, 1967) could follow the seasonal Kiboko River south to the arid area north of Amboseli. *Anubis* baboons from Namanga could follow the seasonal Namanga River, which

flows into the southwestern portion of Lake Amboseli. Or *anubis* baboons from the foothills of Kilimanjaro could follow the seasonal Olmolog River that flows into the southwestern portion of the basin. Because we see the Ositeti Group only during the rainy seasons and only in the southwest, the latter two routes are most likely. Because Ositeti baboons are seen to come from and disappear into the foothills rather than toward Namanga, the third route seems most plausible. However, determination of the actual route of entry of *anubis* baboons into the Amboseli hybrid zone will require further observations.

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