

Baboons of the Amboseli Basin: Demographic Stability and Change

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Received April 10, 1990; revised July 26, 1990

A cross-sectional demographic analysis of the entire baboon population of the Amboseli basin of southern Kenya was undertaken to complement the longitudinal, intensive studies of a subpopulation. The present survey documented the extent and persistence of the influx of anubis baboons into the predominantly cynocephalus community and provided another example of the nonrandom dispersal patterns of cercopithecine males. In addition, the survey confirmed continued demographic stability of the basinwide baboon population and even growth in groups that had access to better feeding conditions, despite decline of the baboons' preferred habitat and expansion of human activities into wildlife areas. Conflicts with activities of humans, however, indicate that the present well-being of the Amboseli baboon population may be short-lived.

KEY WORDS: baboons; demography; food provisioning; human-wildlife conflict.

INTRODUCTION

Research on the demography and behavioral ecology of savannah baboons in Amboseli, Kenya, has produced detailed, longitudinal data for individually identified animals of several groups (Walters, 1980; Hausfater *et al.*, 1982; Altmann *et al.*, 1988). Such long-term, intensive study of a subpopulation is essential for understanding the mechanisms and details of demographic structure. Because behavioral interactions, genetic exchange, disease transmission, and other processes occur over a broader geographic

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range, information about the larger population of which the selected groups are a part is equally important. In only a few studies of nonhuman primates has it been possible to provide demographic data both within groups and across a whole population (Dittus, 1977; Harcourt *et al.*, 1980, 1981; Goodall, 1986). Here we present a cross-sectional demographic analysis for the entire baboon population of the Amboseli basin to complement the longitudinal, intensive studies of the subpopulation.

The goal of the present investigation was to determine whether the recent stability and demographic characteristics of the central basin subpopulation (Altmann *et al.*, 1985) were representative of the larger population. In particular, we sought (1) to identify characteristics of groups within the population that are demographically more successful; (2) to obtain more information on the recent migration of olive baboons into the predominantly yellow baboon population (Samuels and Altmann, 1986); and (3) to expand our measurement of the dispersal area of males.

Amboseli and Its Baboon Population

The Amboseli basin is an area of semiarid savannah in southern Kenya, described in detail by Western (1973), Western and Sindiyo (1972), and Western and van Praet (1973). The basin is the site of an extinct Pleistocene lake, defined by natural physical boundaries. Within the basin, Amboseli National Park, established in 1977, is a 390-km² area containing most of the basin's permanent natural water sources in the form of perennial springs and swamps derived from runoff from Mt. Kilimanjaro.

Wildlife concentrate in the basin during the dry season because of the availability of good late-season forage and permanent water. During the rains, wildebeest, zebra, and other migratory species move into the highlands surrounding the basin, where they can drink from temporary rainpools. Although the basin's natural boundaries are not a barrier to these migratory species, a semiisolated population of savannah baboons resides therein.

Dispersal of the Amboseli baboons out of the basin is limited by ecological barriers (Fig. 1). To the north, Eremito Ridge marks the edge of the ancient lake and the beginning of an extensive waterless scrub plain; the nearest baboon population to the north is more than 80 km away, in the Simba-Kiboko region. To the west, a seasonally flooding relic of the Pleistocene lake separates Namanga baboons from the Amboseli population by 45 km. To the south, mixing between Mt. Kilimanjaro and Amboseli baboon populations is probably infrequent or of recent origin (Samuels and Altmann, 1986). Dispersal of baboons to and from the basin occurs primarily in the east, where a range of hills presents no obstacle to baboon movements.

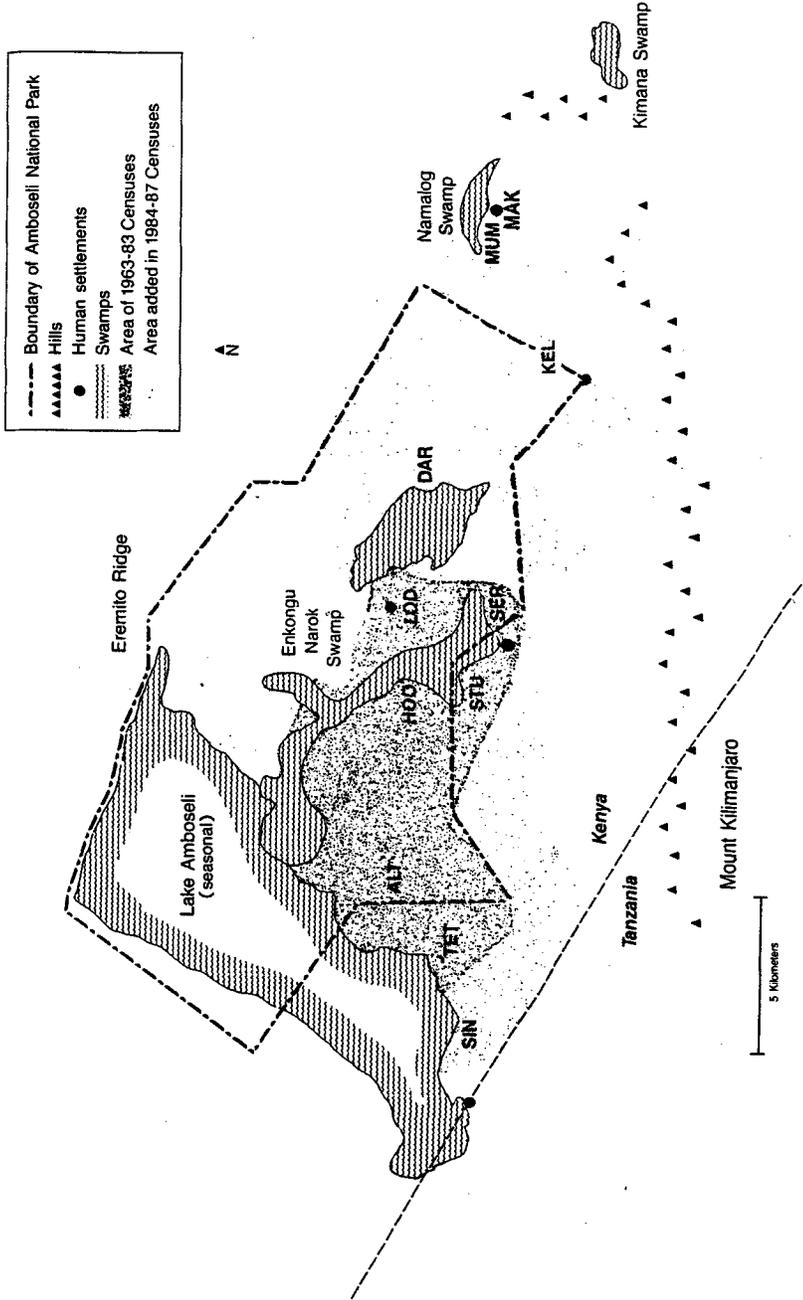


Fig. 1. Map of the Amboseli basin in southern Kenya showing the ecological features that define the basin, the areas of previous and the present surveys, and the locations of the 11 baboon groups surveyed in 1984 and 1987: Alto's (ALT), Olodare (DAR), Hook's (HOO), Olkelumyet (KEL), Lodge (LOD), Olmakau (MAK), Olumweny (MUM), Serena (SER), Sinya (SIN), Stud's (STU), and Ositei (TET) groups. Note that although the entire basin was surveyed in 1984-1987, the shading of the figure indicates only the baboon-habitable areas of the basin (defined in the text).

METHODS

Repeated censuses of the baboons in the central western portion of the Amboseli basin, an area of 68.4 km², from Enkongu Narok Swamp to Nairabala Hill (Fig. 1), were conducted from 1963 to 1983 (Altmann *et al.*, 1985). The present survey encompassed the entire basin, an area of approximately 600 km² (Western, 1973), thus extending the area of the original surveys to include the Sinya area at the Kenya-Tanzania border to the west and the rest of Amboseli National Park and Namalog Swamp to the east. The eastern boundary of the survey is somewhat arbitrary because baboons are continuous from Namalog, within the basin, to Kimana and farther east, outside of the basin. Baboons living in the hills were not included in the present survey, because they are not primary inhabitants of the basin and because much effort would have been required to census these unhabituated and wary baboons in rough terrain.

The basinwide survey was initiated during the short rains of 1984 (November-December), and an additional group was located during the long rains of March 1985. During the dry season of 1987 (June-August), all but the three easternmost groups were censused again. The eastern groups (KEL, MAK, MUM) could not be recensused in 1987 because the expansion of agricultural land into wildlife habitat resulted in conflict between farmers and baboons in the Namalog area.

The censusing technique is described by Altmann and Altmann (1970). Briefly, baboons were visually identified by age and sex as they moved past an arbitrarily chosen counting point in a progression across an open area. Censuses were repeated several times on each group.

The expertise necessary for conducting a basinwide survey and for identifying age/sex classes was gained through regular systematic evaluations of the physical developmental characteristics of immature baboons of known age in the primary study groups and from periodic censusing of groups adjacent to the primary study groups. All members of the primary study groups (ALT and HOO, plus LOD in 1987; see Fig. 1) were individually known as subjects of longitudinal behavioral, ecological, and demographic research. Monitoring the movements and interactions of primary study groups provided us with information on the whereabouts of other groups in the basin. In addition, unfamiliar groups were located by monitoring sleeping or watering places and by consulting Park rangers, researchers, and local Maasai. We are confident that all groups were located because of the intensity and duration of our search and the limited distribution of baboon sleeping and watering sites in Amboseli.

Demographic Categorization

We recorded the age of all individuals and the sex of all adults. Each adult male was scrutinized to determine whether he was one of those known to have emigrated from the primary study groups during 1982–1987. Developmental classes were defined and distinguished as by Altmann *et al.* (1981), with the exceptions that the two infant classes and two juvenile classes were each combined into single classes: “infant/yearling” and “juvenile.”

Individuals for which complete information was not attainable were classified according to the class distribution of individuals in those baboon groups for which there were no unknown individuals. This method resulted in some underestimation of intergroup variability, but the proportion of unclassified individuals was small. In the 1984 survey, only 2.5% of individuals were of unknown age/sex class; their classification was based upon complete information obtained for six groups. In 1987, complete information was obtained for all individuals.

Because baboons are a relatively polygynous species in which females typically outnumber males among sexually mature animals (Altmann and Altmann, 1970), we tested for equal sex ratios among adults. Because declining populations of macaques, primates with life stages similar to baboons, are reported to have a deficit of immature animals (Southwick and Siddiqi, 1976, 1977), we tested for equal prevalence of immature and mature animals. Comparisons of demographic classes are reported as ratios to conform to the literature, e.g., a group comprised of 1.0 female per male contains equal numbers of females and males.

For evaluation of the demographic condition of a group, Altmann *et al.* (1985) concluded that “an older juvenile class that is one-half the size of the adult female class is one that would provide replacement but not growth” in a baboon population with rates of maturation and adult female mortality as found in ALT (Altmann, 1980, unpublished data). However, recent data on LOD (J. Altmann *et al.*, unpublished) and on other semiprovisioned cercopithecines (reviewed by Altmann, 1986; Fa and Southwick, 1988; Asquith, 1989) confirm that maturation is accelerated and adult mortality is reduced under conditions of food enrichment. Differences in these demographic parameters will change the size of the juvenile class that will be adequate for replacement and will serve as an indicator of demographic health. Consequently, to evaluate demographic condition in the absence of longitudinal data for each group in the present survey, we simply report actual adult female replacement in each of the primary study groups, representing three of the feeding conditions.

Taxonomic Categorization

Savannah baboons have been designated separate species (Maples and McKern, 1967; Napier and Napier, 1967). Nonetheless, several types are able to interbreed and some taxonomists (Buettner-Janusch, 1966; Jolly and Brett, 1973) accord them subspecific status. The Amboseli baboon population consists primarily of yellow baboons, *Papio cynocephalus* or *P. cynocephalus cynocephalus*, hereafter referred to as yellow or *cynocephalus*. Beginning in 1982, olive baboons, *P. anubis* or *P. cynocephalus anubis*, hereafter referred to as olive or *anubis*, became a small but persistent component of the basin population. Evidence for a new or unstable *cynocephalus-anubis* hybrid zone in southwestern Amboseli is presented by Samuels and Altmann (1986).

During the survey of the Amboseli basin, each animal was scrutinized to determine its taxonomic type: among adults and juveniles, yellow baboons are visually distinct from olive baboons by coat color, facial characteristics, length of cheek and mantle hair, and body shape (Maples and McKern, 1967; Kingdon, 1974). We were unable to identify visually the taxonomic type of yearlings and infants.

Neighboring baboon populations to the south and west are *anubis* [Mt. Kilimanjaro (B. Oguya and D. Western, personal communications); Namanga (Maples and McKern, 1967; personal observation)]. The Simba-Kiboko baboons to the north are *cynocephalus-anubis* hybrids (Maples and McKern, 1967). Baboons living in Kilmana and further east are *cynocephalus* (van Citters *et al.*, 1967; Altmann and Altmann, 1970).

Categorization of Feeding Condition

Baboon groups of the Amboseli basin were classified according to feeding condition by a general assessment of the quality and distribution of food resources. Groups that fed entirely upon natural foods were further divided into "savannah groups" that range primarily in dry savannah areas and "swamp groups" that range primarily in lush swamp regions. Other baboon groups obtained a significant portion of their diet from human foods in addition to natural foods. For groups classified as "garbage-feeding groups," provisioning occurred at the open garbage pits of tourist facilities, where discarded human foods were regularly available to baboons and other wildlife. Another form of provisioning occurred at the eastern edge of the basin, where the Amboseli Maasai are shifting their livelihood from nomadic pastoralism to sedentary agriculture and where land traditionally shared by wildlife and livestock is being converted to small farms. In these

new agricultural areas, "crop-feeding groups" supplemented their diets with cultivated maize, onions, and tomatoes.

Statistical Tests

Testing was done against a binomial hypothesis of equiprobability ($p = q = 0.50$), using a significance level of 0.05, two-tailed, to examine sex distribution among adults, proportion of immature animals, and changes in group size.

RESULTS

Characteristics of the Amboseli Baboon Population in 1984

A total of 11 baboon groups was found in the Amboseli basin in 1984 (Fig. 1). Six of them fed entirely upon natural foods: savannah groups ($n = 4$)—ALT, KEL, SIN, and TET; and swamp groups ($n = 2$)—DAR and HOO. Five groups supplemented their diet with human foods: garbage-feeding groups ($n = 3$)—LOD, SER, and STU; and crop-feeding groups ($n = 2$)—MAK and MUM.

The density of the 476–479 baboons of the basin was 1.15 baboons per km² within the approximately 416 km² of baboon-habitable land, loosely defined as areas of *Acacia* woodlands and permanent waterholes. Seven of the 11 groups, or 282–284 baboons, ranged partially or entirely within the boundaries of Amboseli National Park, while the far-western (SIN, TET) and far-eastern (MAK, MUM) groups were never observed within park boundaries. Within the 390-km² park, the density of baboons could have been as great as 0.73 baboon per km²; but the actual density at any time was probably lower because only four baboon groups (DAR, HOO, LOD, SER), or a total of 134–136 baboons, ranged primarily within park boundaries. At least half of the ranges of each of the other groups (ALT, KEL, STU) were outside of the park.

Group size varied from 17–18 to 77 individuals (Fig. 2). Median group size was 39 baboons: median size of each age/sex class was 7 adult males, 2 subadult males, 12 adult females, 9 juveniles, and 8 infants/yearlings.

Group composition varied from one multifemale/single-male group to multifemale/multimale groups and included one group in which the number of adult females was exceeded by the number of adult males (SIN; sex ratio = 0.93 female per male). A significant number of groups had female-biased adult sex ratios ($n = 11$ groups, $p = 0.006$); and overall, adult

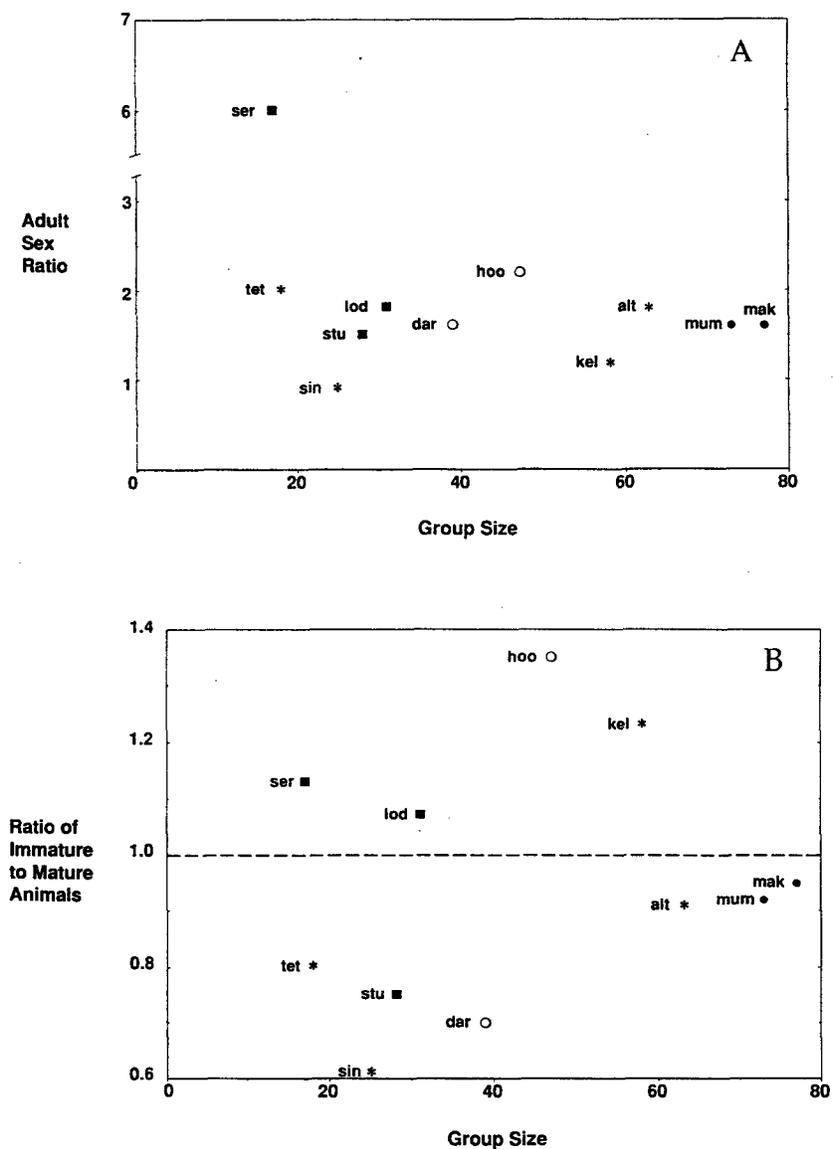


Fig. 2. The relationship in 1984 of group size to (A) the ratio of adult females to adult males and (B) the ratio of immature to mature animals. Feeding conditions are indicated by asterisks for savannah groups, open circles for swamp groups, filled circles for crop-feeding groups, and filled squares for garbage-feeding groups.

females significantly outnumbered adult males in the population (sex ratio of all groups pooled = 1.62 females per male, $n = 223$ adults, $p < 0.001$). In only one group, however, did the number of females significantly differ from the number of males (SER; sex ratio = 6.0, $n = 7$, $p = 0.016$; see Fig. 2A).

Adult sex ratio was unrelated to group size (Spearman rank correlation coefficient $r_s = -0.116$, NS) but was related to feeding condition. Although savannah groups had a low combined adult sex ratio (1.42 females per male; $n = 78$, NS), females significantly outnumbered males in crop-feeding groups (sex ratio = 1.57, $n = 70$, $p = .05$, swamp groups (sex ratio = 1.86, $n = 40$, $p = .038$), and garbage-feeding groups (sex ratio = 2.0, $n = 36$, $p = .028$).

Approximately half of the population consisted of sexually mature animals, i.e., adult and subadult males and postmenarcheal females; overall, the ratio of immature to mature animals was 0.95. Group composition ranged from 0.61 to 1.35 immature to mature animals; but no group or feeding condition differed significantly from equal proportions of immature and mature members (see Fig. 2B).

Presence of Olive Baboons

More than 95% of juveniles and adults of the Amboseli baboon population in 1984 were yellow-type baboons. The remaining baboons (15–17 of 380 juveniles and adults) were *anubis* in appearance and were found only in the three westernmost groups.

All *anubis* members of ALT and SIN were males. Two *anubis* males (one adult, one older juvenile), known to be immigrants, were present in ALT, and five *anubis* males (three adults, one subadult, one older juvenile) were found in adjacent SIN.

Anubis females were present only in TET. More than half of the members of TET were *anubis* in appearance, including at least two juveniles and at least four of the six adult females. Two adult females could not be classified, because although they were yellow in coat color, the features of their faces, bodies, and tails were more *anubis*-like; they probably were hybrids.

Changes in the Characteristics of the Amboseli Baboon Population, 1984 to 1987

Eight of the 11 baboon groups, a total of 325–327 baboons, were censused again in 1987. We were unable to survey again the three easternmost

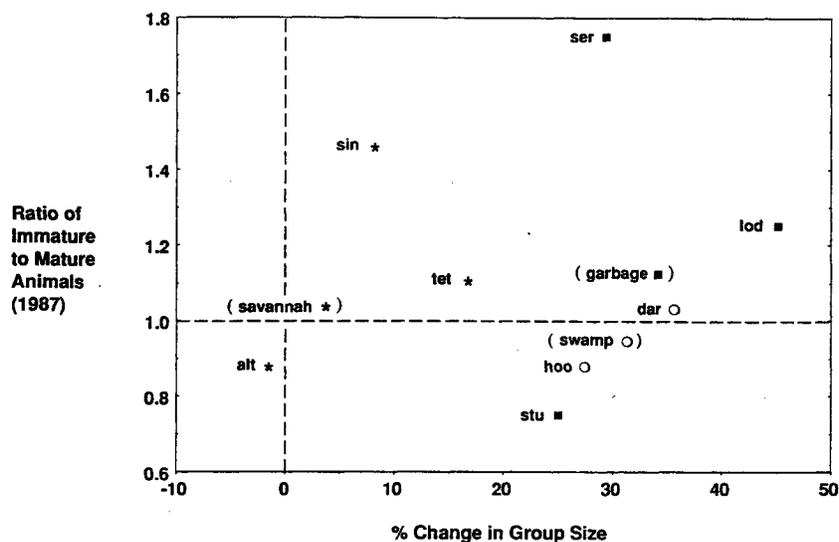


Fig. 3. The relationship of the change in group size from 1984 to 1987 to the ratio of immature to mature animals in 1987. Feeding conditions are indicated as in Fig. 2.

groups, which had been among the largest groups in the population in 1984 and which included both crop-feeding groups.

In 1987, the distribution of *anubis* baboons was similar to that of 1984. More than 95% of adults and juveniles of the eight groups censused again in 1987 were yellow-type baboons, and *anubis* baboons were found in two of the three western groups in the basin. Although no *anubis* members were in SIN at the time of the 1987 census, *anubis* males were seen with the group within the 6 months preceding and following the survey.

Nearly all groups censused again in 1987 showed an increase in group size over the 2.5-year period ($n = 8$ groups, $p = 0.035$); five of those groups increased in size more than 20%. Groups in better feeding conditions showed greater increases in group size (Fig. 3). The three groups that habitually fed on garbage showed an overall increase of 34.2%, and the two groups that ranged primarily around the central swamps increased 31.5%, whereas the three groups that ranged predominantly in dry savannah regions showed only 3.8% increase in group size.

Although an increase in group size was associated with feeding condition, we could identify no single demographic process that would account for the observed population growth (Fig. 3). The 57 "additional" animals in the recensused portion of the population represented all age/sex classes: 5 adult males, 5 subadult males, 9 or 10 adult females, 30 or 31 juveniles,

and 7 infants/yearlings. Several groups with the greatest growth showed increases in numbers of immature animals and/or adult females. Increases in the number of adult males were observed only in the two swamp groups.

Although the proportion of immature animals within the population, and particularly within garbage-feeding groups, was higher in 1987 than in 1984, the proportion of immature animals in 1987 was not significantly different from the proportion of mature animals within the population as a whole, within any feeding condition, or within any group. However, significantly more of the "additional" animals in the population were immature than the expected one-half (ratio = 1.92 immature per mature animals, $n = 57$, $p = .012$). Garbage-feeding groups tended to have large cohorts of infants/yearlings, and large numbers of juveniles were found in swamp groups and a garbage-feeding group.

Growth in garbage-feeding and swamp groups was associated also with increases of adult females. In contrast to the 1984 survey in which females outnumbered males in only one group, two garbage-feeding groups and a swamp group had significantly more adult females than adult males in 1987 (LOD, sex ratio = 2.4 females per male, $n = 17$ adults, $p = 0.047$; SER, sex ratio 7.0, $n = 8$, $p = .031$; HOO, sex ratio = 2.1, $n = 28$, $p = 0.026$), despite stable or increasing numbers of adult males. In particular, the overall adult sex ratio of garbage-feeding groups increased from 2.0 females per male in 1984 to 2.5 in 1987 ($n = 42$, $p = .002$).

To estimate adult replacement under different feeding conditions, we compared, for each of the three primary study groups, the actual number of females that entered each group through maturation relative to the number that left through death, during the time period for which we had longitudinal data. ALT, a savannah group that remained stable in size, had equal numbers of females that matured ($n = 12$) and that died ($n = 11$) over a 7-year period. HOO, a swamp group that increased in size, had twice as many females that matured ($n = 13$) as died ($n = 6$) over a 7-year period. LOD, a garbage-feeding group that increased in size, had three times as many females that matured ($n = 3$) as died ($n = 1$) over a 3-year period.

Male Dispersal Within the Amboseli Basin

An adult male that disappears may die suddenly within his group or he may leave the group. An emigrating male may then die, live alone for a considerable period, or join another group. In many cases, these events cannot be distinguished with certainty, but for nearly all cases presented below, we are able to rule out death before leaving the group.

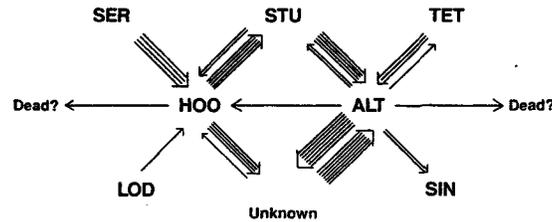


Fig. 4. The direction of migration of males leaving or entering ALT and HOO groups from September 1982 through July 1987, including males of unknown fate or origin. Each line represents one migration event. The home range of ALT overlaps with those of HOO, SIN, STU, and TET; the home range of HOO overlaps with those of ALT, LOD, SER, and STU.

From September 1982 through July 1987, there were 49 migration events involving 37 males to or from two primary study groups, ALT and HOO. Eleven of the 24 departing males (46%) went to known destinations, and 17 of the 25 immigrants (68%) were from known origins. In all cases of known origin or destination, migrants came from or went to an adjacent group (Fig. 4).

Of the 13 males that emigrated to unknown destinations, 2 probably died: a crippled male disappeared on a morning when lions were nearby (recorded by R. and B. Noe) and an old male was last seen alone, injured, and emaciated (recorded by R. S. Mututua and S. Altman). None of the remaining 11 migrant males of unknown destinations were found in either basinwide survey, i.e., the four males that disappeared before the 1984 survey were not located 17 to 97 weeks after their departures; the seven males that disappeared between the 1984 and the 1987 surveys were not located 13 to 117 weeks after their departures.

Solitary males are uncommon but do exist in the Amboseli population. In the 1984 survey, a solitary adult male was observed on a number of occasions to sleep and travel by himself, and he visited the garbage pit at a ranger outpost for several months. He was seen always within the home range of KEL and, in March 1985, joined KEL. We know little about the nature or duration of his solitary period, but we know more about two other males born in primary study groups that became solitary during the interim between censuses. Each male left his natal group at age 8–9 years, remained solitary for 8 months, then joined a group adjacent to his natal group. Each male was seen repeatedly during his period of solitary life, remaining within the range but rarely within the immediate proximity of his natal and destination group.

DISCUSSION

The present survey, drawn from a wide geographic area, complemented the more focused, long-term studies of selected groups within the baboon community of the Amboseli basin (Altmann *et al.*, 1981, 1985). In particular, the present survey (1) documented the persistence and extent of the influx of *anubis* baboons into the predominantly *cynocephalus* community (Samuels and Altmann, 1986); (2) provided an additional example of the nonrandom dispersal pattern of cercopithecine males (Packer, 1979; Cheney and Seyfarth, 1983); and (3) confirmed the continued stability of the basinwide population (Altmann *et al.*, 1985). The survey also allowed us to identify some characteristics of groups within the community that were demographically more successful.

Gene Flow into and Within the Population

Since 1982, *anubis* baboons have remained a small but persistent component of the Amboseli basin population. Baboons that were *anubis* in appearance were found only in the three groups that range in the southwestern portion of the basin. *Anubis* members of TET included both males and females, whereas all *anubis* members of the other groups were male. Because females are the sex that does not disperse, we concluded that TET was an *anubis* group into which *cynocephalus* males had immigrated. Our supposition that the *anubis* community on Mt. Kilimanjaro was the source of the *anubis* invasion into the basin (Samuels and Altmann, 1986) was supported by more recent observations of TET in the foothills beyond the southwestern edge of the basin. The recent appearance of *anubis* baboons in Amboseli may result from a shift in the ranging patterns of *anubis* baboons of the foothills due to expanding agricultural activities on the slopes of Kilimanjaro (Lovatt Smith, 1986, personal observation). Such a shift would facilitate exchange of males between basin and foothill communities. Current genetic studies of the Amboseli baboons, and of baboon populations elsewhere, may assist in the interpretation of the extent of *anubis* influence within Amboseli.

Patterns of male dispersal within the basin population also affect population structure. Despite extensive searching to determine the dispersal range of male baboons of Amboseli, the only migrant males that we located were those that moved to groups immediately adjacent to their group of origin. Among cercopithecines, movement of males primarily between adjacent groups has been documented also for vervet monkeys (Cheney and Seyfarth, 1983) and *anubis* baboons (Packer, 1979). Our lack of success in

locating all emigrating males suggests that males not found in adjacent groups either died or traveled long distances and left the community. Circumstantial evidence indicates that both suppositions are correct: two males disappeared while they were ailing; in addition, a known lone male was found on a waterless plain at the edge of the basin (recorded by R. and B. Noe), more than 20 km from his group of origin (HOO). Ongoing research focuses on the behavior of male baboons and on patterns of dispersal within the Amboseli community.

Effects of Behavioral Flexibility on Demographic Processes

The present survey confirmed that the Amboseli baboon population continues to be stable in size and that the stability is basinwide. A dramatic decline in baboon numbers in the 1960s and early 1970s, followed by stabilization in the mid-1970s, was revealed by demographic analyses based on repeated censuses of the central basin subpopulation (Altmann *et al.*, 1985). The present survey verified that the stability indicated in the geographically limited but longer-term analyses of groups in the central basin is representative of the status of the entire basin community.

The present overall stability of the Amboseli baboon population is surprising in view of dramatic ecological changes ongoing in the Amboseli basin, in particular the continued decline of the fever tree, *Acacia xanthophloea*, woodland (Western and van Praet, 1973; Altmann, 1977; Western, 1983; Lovatt Smith, 1986). Local populations of several wildlife species have been affected adversely by loss of habitat, including vervet monkeys (Struhsaker, 1973, 1976; Cheney *et al.*, 1988).

The tenacity of the baboons, despite the decline of their preferred fever tree habitat, may result in large part from their behavioral flexibility. Over the past decade, we observed major, though gradual, shifts in the home ranges of several baboon groups in the basin away from areas of fever tree die-offs to new areas where healthy fever tree woodlands remain.

Change of range by other baboon groups has been possible through exploitation of new resources. For example, although baboons in Amboseli typically sleep in fever trees (Altmann and Altmann, 1970), some groups recently began to utilize other tree species for sleeping. On only one occasion (recorded by R. and B. Noe) before 1984 were baboons observed to sleep in trees other than *A. xanthophloea* (Amboseli longitudinal data base, unpublished). By 1987, however, at least three baboon groups were frequently sleeping in *A. tortillis* trees as well, and 15 *tortillis* sleeping groves had been added to a comprehensive list of more than 110 *xanthophloea* sleeping groves compiled since the early 1970s (S. Altmann, unpublished).

data). A few groves of another *Acacia* species and *Syzygium guineensis* are now used as well.

The success of baboons in diverse ecosystems has been attributed in part to their eclectic feeding habits with respect to natural foods (Norton *et al.*, 1987). Exploitation of human foods is another example of the behavioral flexibility of baboons. Nearly half of the groups in the Amboseli basin have discovered and are coming to rely upon this new resource. Inadvertent provisioning of wildlife with cultivated crops is spreading with the expansion of farmland in the basin. Farms first appeared in Namalog in the early 1980s and the human population grew rapidly to more than 1000 by 1987 (D. Maitumo, personal communication). Resident wildlife species of Namalog Swamp, including baboons, now supplement their diets with cultivated crops, despite efforts by farmers to eliminate crop-raiding pests that threaten their livelihood.

In addition, as the human population within the park has increased steadily, there has been a corresponding increase in the availability of garbage to baboons and other wildlife. Only a single group of baboons fed on garbage in 1982, while 5 years later, three baboon groups obtained much of their nourishment from discarded human foods. In Amboseli, garbage continues to provide a portion of the diet of many wild animals including baboons, despite limited success of numerous garbage-management schemes.

While the baboon population remained stable overall, certain groups within the population increased in size during the interim between censuses. Increases in group size were associated with better feeding conditions, but we were unable to pinpoint a single demographic process as causal. The maturation of a large cohort of infants born after the 1984 drought may have inflated temporarily the number of immature animals. However, from recent studies of a garbage-feeding group (J. Altmann *et al.*, unpublished data), we now know that in semiprovisioned conditions, youngsters mature more rapidly and females reach sexual maturity at an earlier age and have accelerated reproductive rates, relative to their peers in wild-feeding groups (Fa and Southwick, 1988; Asquith, 1989). Reduced adult mortality and accelerated rates of maturation and reproduction no doubt contributed substantially to the observed growth of groups that had better feeding conditions.

Moreover, accelerated maturational rates may explain biased adult sex ratios that we found in groups in better feeding conditions. Females of LOD mature into the adult class at an earlier age, while male maturation and dispersal from LOD are not comparably accelerated (J. Altmann *et al.*, unpublished data), resulting in a pattern of adult sex ratios skewed toward females. In poor feeding conditions, the converse may be true: for example,

following severe food and water shortage, the adult sex ratio within a community of chacma baboons shifted to favor males (Hamilton, 1985).

An additional consequence of differential maturational rates is that, for different feeding conditions, age class membership based upon visual criteria, as was used in this survey and others, is more likely to be equivalent to developmental rather than chronological age. Thus estimated ages of immature animals in groups that receive food provisioning may be biased upwards.

Consequences of Food Provisioning

Availability of predictable, concentrated, high-quality food resources such as garbage and crops is a mixed blessing for baboons and other wildlife. Provisioning that is carefully planned may be employed to enhance conservation efforts (Lyles and Dobson, 1988; Asquith, 1989). More typically, provisioning is inadvertent, and the short-term benefits may be offset in the long run by gradual alterations in behavior, social organization, and demographic structure (Lee *et al.*, 1986; Altmann and Muruthi, 1988; Fa and Southwick, 1988; Asquith, 1989). Such alterations can be life-threatening if, for example, youngsters do not learn how to find and process natural foods or precocious mothers do not learn the skills needed to care for their offspring (Altmann, 1986). Benefits afforded by provisioning are more immediately counteracted when feeding on rich, contaminated, or concentrated foods results in disease or health risks (Wrangham, 1974; Rolland *et al.*, 1985; Sapolsky and Else, 1987) or when the inevitable direct conflict with humans occurs. Baboons that feed on human foods eventually become dangerous to or threaten the livelihood of the humans with whom they come into contact, and "problem" monkeys are frequently destroyed (Else and Eley, 1985; Lee *et al.*, 1986; but see Strum, 1987).

Behavioral flexibility of baboons has enabled them to adapt to the ongoing ecological shift from *Acacia* woodland to grassland habitat and to the encroachment of human populations into wildlife habitat. Despite the adaptability of the baboons, the stable status of the Amboseli population may be short-lived. Although some groups in the population appear to be thriving, we suspect that crop-feeding groups are declining, as has occurred in primate populations in other agricultural areas (Southwick *et al.*, 1983). We were unable to reevaluate the status of Amboseli crop-feeding groups because those baboons became unapproachable when farmers began to kill them. Behavioral adaptations of baboons, such as feeding on human foods, that we found to be associated with demographic success in the short term,

are the very same behaviors that, in the long term, put baboons on a collision course with human development.

ACKNOWLEDGMENTS

This research is the result of the combined efforts of the Amboseli Baboon Research Project, the Institute of Primate Research (IPR) of the National Museums of Kenya, and the Kenya Wildlife Conservation and Management Department (WCMD), now the Kenya Wildlife Service. We thank J. G. Else, former IPR director, D. M. Sindiyo, former WCMD director, B. Oguya, former warden of Amboseli National Park, and our Amboseli Baboon Project colleagues, S. C. Alberts, P. Muruthi, R. S. Mututua, and V. S. Sikawa. We are grateful to those who shared with us their knowledge of Amboseli and its wildlife, including the people of Namalog; wildlife rangers and tour guides of Amboseli; and P. C. Lee, J. H. Poole, D. Western, and especially J. P. Leboo. We particularly acknowledge the persistent efforts to prevent wildlife from feeding on garbage made by the staff of the Ololarashi-Olgulului Group Ranch Campsite and by K. Lindsay and fellow Amboseli researchers. S. C. Alberts, S. A. Altmann, and P. Muruthi made helpful comments on the manuscript; L. Fitzgerald, K. Mozdzierz, L. Perfect, and C. Saunders helped with figure preparation; and L. Reiter helped with manuscript preparation. The Woods Hole Oceanographic Institution provided facilities for AS during the final manuscript preparation. This research was supported by Grant MH15007, National Geographic, and the Chicago Zoological Society.

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