

*Euclid O. Smith*

Department of Anthropology,  
Yerkes Regional Primate Research  
Center, Emory University,  
Atlanta, Ga., USA

## **Dispersal in Sub-Saharan Baboons**

### **Key Words**

Dispersal  
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Savanna baboons  
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Mating system  
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### **Abstract**

In most mammalian species, males tend to leave their natal group and disperse farther than females, while females tend to be philopatric. Primates generally follow this rule, although long-term studies of a variety of species are revealing an increasing number of exceptions. This paper reviews dispersal patterns in 3 subspecies of savanna baboons (*Papio cynocephalus cynocephalus*, *P. cynocephalus anubis*, *P. cynocephalus ursinus*) which exhibit very similar patterns of social organization. Males usually disperse from the natal group at 8–10 years of age. Female dispersal is rare but well documented. Inbreeding avoidance as well as enhanced mating opportunities are suggested as ultimate causes of dispersal. Several proximate factors implicated in the timing of dispersal events are also reviewed.

### **Introduction**

Patterns of dispersal have a profound impact on genetic structure, population dynamics and social behavior [1–5]. Among mammals, including nonhuman primates, males more often disperse from their natal group and typically disperse over greater distances than do females [6, 7]. However, there is a small number of species in which females regularly transfer to other breeding groups during adolescence while males exhibit natal phi-

lopatriy, e.g. chimpanzees and spider monkeys [8]. Finally, there are a few species that live in either one-male or multi-male groups in which both sexes disperse from their natal group at puberty and transfer into other breeding groups, e.g. red howlers, mantled howlers and some populations of red colobus [9–11]. Emigration from the natal group and immigration into a breeding group are thought to be among the most important and risky behaviors undertaken by dispersing animals, but there have been relatively few at-

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Euclid O. Smith, PhD  
Department of Anthropology  
Emory University  
Atlanta, GA 30322 (USA)

tempts to quantify the costs and benefits of dispersal on the basis of detailed data. Although there are important gender and species differences, emigration and transfer are virtually ubiquitous in group-living nonhuman primates. In this paper, I review data bearing on both the proximate and the ultimate causes of dispersal in sub-Saharan baboons. As far as possible, I identify costs and benefits not only to the dispersing individual but also to individuals in the disperser's group. The dispersal of certain individuals may yield fitness benefits to other group members as well as to the migrants themselves.

I follow here the general definitions provided by Shields [12] and use 'dispersal' for the movement of an organism from its group of origin immediately into a breeding group. Following Pusey and Packer [13], I refer to 'transfer' as any further migration between breeding groups following the initial dispersal.

Rather than attempt another survey of dispersal and philopatry for all primates, I review available data regarding dispersal in sub-Saharan *Papio*. My comments are restricted to a discussion of dispersal in species typically labelled 'savanna' baboons (*Papio cynocephalus cynocephalus*, *P. cynocephalus anubis*, *P. cynocephalus ursinus*), which all exhibit similar patterns of social organization. I exclude both hamadryas baboons (*P. hamadryas*) and geladas (*Theropithecus gelada*) from the discussion, because of the obvious differences in social organization, although similarities in patterns of social relationships exist [14]. Baboons are among the best-studied nonhuman primate species and provide an excellent illustration of certain principles associated with male dispersal. Because of the numerous field studies of baboons, it is important to consolidate information on dispersal into a single review. I also provide a brief discussion of

female dispersal in baboons, a phenomenon that occurs infrequently and then only under unusual ecological conditions. While baboons are typically characterized as a 'male-dispersing species', the fact that females emigrate under particular circumstances calls for critical thinking about the costs and benefits of transfer and dispersal.

### Evolutionary Explanations

Two contrasting evolutionary explanations have been proposed for dispersal from the natal group in primates generally and in baboons in particular. First, outbreeding as a means of avoiding inbreeding depression has been postulated as a major factor in the promotion of male dispersal [15–20]. The deleterious consequences of inbreeding are well known and include an increase in homozygosity and a consequent loss in fitness [21], inbreeding depression in normally outbred populations [6, 22] and increased susceptibility to pathogens [23]. The view is widely held that inbreeding avoidance is largely responsible for dispersal from the natal group in baboons, although only one field study has provided data apparently demonstrating the fitness-reducing properties of inbreeding [19]. Clear evidence for inbreeding depression has been obtained only from captive primate populations [22]. Inbreeding costs are undoubtedly important factors driving the dispersal system, but they are probably not the only factors involved.

Alternatively, Moore [24] and Moore and Ali [25] argue that male dispersal is not due to inbreeding avoidance but is caused by competition for mates. Intrasexual competition appears to be a major factor in dispersal in species that typically live in one-male groups, e.g. in female howler monkeys and in male and female gibbons. It does not seem to be a factor

in species for which dispersal from the natal group appears to be voluntary (e.g. baboons), although there is evidence for considerable male-male competition [26]. Moore [24] and Moore and Ali [25] argue for primates in general that, by dispersing from the natal group, males are actively seeking improved mating opportunities. However, there are data that suggest that some males, savanna baboons in particular, do not leave their natal troop at maturity and actually spend all or a large part of their reproductive careers there [27]. Packer [19], Moore [24] and Moore and Ali [25] all agree that secondary transfers are timed not to avoid consanguineous mating but to increase mating opportunities. Differences between these positions, then, center on the underlying cause of male dispersal from the natal group.

In order to address the question of the ultimate causation of male dispersal, including both initial dispersal from the natal group and secondary transfer, it is important to consider some of the proximate factors that might play a role either in triggering dispersal from the natal group or in the timing of secondary transfers. It is much easier to study factors implicated in the decision to leave a group ('push factors'), but we have a less clear idea of the factors implicated in a decision to move to a particular group ('pull factors'). This is largely because push factors can be studied in one group, while observation of multiple groups is required to illuminate pull factors. In this review I examine both factors to the extent that the data allow.

### **Aggression and Dispersal**

The role of agonistic behavior as a causal factor in emigration varies across species but does not appear to be an important factor for dispersal from the natal group in baboons

[19]. Field workers have not reported periods of high levels of aggression directed at males prior to emigration from the natal group. On the contrary, most authors have commented on the lack of aggressive challenges to such males just prior to emigration [28]. Emigration without coercion is certainly common among baboons, and the lack of aggression applies to both dispersal from the natal group and secondary transfers.

Many field workers have noted that immigrant male baboons are met with aggression from resident males. Resident males that had previously transferred from the same natal group as the immigrant were the most likely perpetrators of aggression, particularly if they were of approximately the same age as the immigrant [19]. On the other hand, there have been reports of cases where immigrants met with little or no opposition [29-33]. Ransom [31] saw little aggression against newcomers among the Gombe baboon groups he studied. Similar results were also reported by Rowell [32, 33] as well as by Anderson [29] for troops inhabiting very different ecological contexts. The factors responsible for variation in expression of aggressive behavior towards dispersing males are unknown. Some combination of demographic effects and local ecological conditions is probably involved.

Perhaps male baboons must balance the costs of dispersal (risk of predation, targeted aggression by resident males, risk of inbreeding depression, potential loss of breeding opportunities with known females without risk) against the benefits of emigration (new mating opportunities and hence reduced probability of lowered fitness due to inbreeding). Local conditions and social milieu are likely to influence the cost/benefit ratio.

## Agonistic Rank and Dispersal

Appreciable evidence indicates that dominance rank affects the likelihood of dispersal from the natal group as well as secondary transfer in males. At Amboseli, Kenya, most immigrant males attain their highest lifetime rank within the first 30 days of transfer, and virtually all achieve their highest lifetime rank within the first 6 months. Attainment of high social rank was found to be a good predictor of tenure. Males in the top half of the hierarchy were much more likely to remain in the group than males in the lower half. The median tenure for high-ranking males was 67 months, while low-ranking males remained in the group for a median period of 18 months [27]. Strum [34], at Gilgil in northern Kenya, found that newly transferred males were winners in agonistic encounters with resident males and were routinely able to displace resident males at preferred feeding sites but had reduced mating success compared to resident males. Newcomer males resorted to aggression, while resident males used less aggressive, cooperative tactics to establish consortships with females. Packer [19] observed that some natal males in the Gombe baboon population in Tanzania attained high rank prior to emigration but, nonetheless, seldom consorted with adult females at midcycle. Hamilton and Bulger [35], for the Okovango Botswana baboon population, report that males in their natal groups rose steadily in rank during the 18 months prior to emigration in three groups of chacma baboons, while upon entry into a new troop they showed a dramatic rapid increase in rank if the transfer was successful. Similar phenomena have been observed with olive baboons at Amboseli, where young males in their natal groups also rose slowly in rank prior to emigration [27]. Bulger and Hamilton [36] report that males that did not leave their natal group in fact behaved as

if they were immigrants, rising rapidly instead of showing slow, steady rank increases. It is tempting to speculate that these males may be testing themselves before either emigrating from the natal group or making a challenge for breeding status within the natal troop.

## Sex Ratio, Sexual Behavior and Dispersal

For dispersal from the natal group, the attraction to novel mating partners appears to be a powerful force in determining emigration. Rather than the number of sexual partners, the number of cycling females or the ratio of cycling females to males (as is the case with secondary transfer), for males transferring from the natal group it is probably simply the presence of novel individuals of similar age and opposite sex. Rasmussen [37, 38] observed that the greatest numbers of both emigrations and immigrations occurred when there was a maximum number of estrous females. He fails to note, however, whether immigration was quickly associated with high levels of sexual activity on the part of the immigrant males. Packer [19, 39] noted new immigrants consorting with females on their first day in the troop. Bercovitch [26] also observed immigrant males in consort shortly after entering the troop. These observations generally support the interpretation that immigrant males are viewed as novel sexual partners by resident females. However, if males do not form consortships soon after arrival, then it suggests that estrous females are not playing a major role in influencing the timing of immigrations. Indeed, as Manzillo [28] notes, females that are cycling when a male enters a troop are likely to be pregnant by the time he is able to hold a consort. Her data suggest, then, that it is not immediate reproductive benefit that is implicated in

male transfer but a potentially more favorable long-term mating climate.

Young males in three Old World monkey species (vervets, long-tailed macaques and rhesus monkeys) seem to emigrate preferentially with peers or older brothers [13]. Unlike these Old World monkeys, male baboons do not disperse preferentially into troops with kin. Both Strum [40] and Smuts [41] observed that more than one male transferred from a single troop into an adjacent troop, but the pattern of kin-related individuals aiding in the transfer process was not observed. Packer [19] also reported that almost all male baboon transfers occurred between adjacent groups. Hence it is likely that males transfer into troops that may very well contain related individuals, but there are no known instances of kin-directed altruism in baboons.

Females can influence the probability of male transfer during intergroup encounters. Smuts [41] observed an estrous female entice a male from an adjacent troop to transfer into her troop. Packer [19] reported that, during intergroup encounters, consorting females would lead partners into the other troop while presenting to newcomers. In addition to solicitations, copulations between females and extragroup males have also been reported. Frequent intertroop encounters may provide the opportunity for high levels of social interaction between group members and, hence, the increased probability of male migration, under certain circumstances [37].

Female acceptance is obviously critical to successful male immigration at a reproductive level. Females seem to play a role in determining whether male immigrants become targets of aggressive behavior by resident males. Smuts [41] found that male olive baboons avoided least by adult females were most likely to remain with the group. In addition, females may be regulating the success of immigrant males in order to gain a competi-

tive advantage over other groups of females, since group size plays an important role in determining the outcome of intergroup competition for resources [42]. However, neither Manziolillo [28] nor Harding [43] could confirm this prediction for the Gilgil baboon population.

### **Age and Dispersal**

Dispersal from the natal group typically occurs in most 'male-dispersing' species at about the time of puberty, although male savanna baboons may delay departure until well after this age. Male yellow baboons typically do not emigrate from the natal group until they are almost fully adult (8-10 years of age), although Manziolillo [28] and Bercovitch [26] report immigration of considerably younger males. By remaining in the natal group until adult size has been attained, a young male may maximize the probability that he can transfer successfully. Altmann et al. [44] note that a male savanna baboon that exhibited retarded growth was not successful in transferring from his natal group to a breeding group. This presumably occurred because he was not able to compete with resident males or, alternatively, because females did not attempt to form social relations with him as he was not perceived to be a fully adult male. Migrating males in prime condition are best able to compete with resident males for access to females. Packer [19] suggested that males transferred into troops having the smallest number of resident males of a similar age in an attempt to avoid high levels of aggression from potential reproductive competitors.

Male age affects secondary transfer. Older, previously transferred males may attenuate aggressive responses of resident males by rapidly forming consortships with estrous fe-

males. Packer [19] found that the average rate of consort activity of previously transferred males was significantly higher than that of males that had transferred directly from the natal group. Older males were found to develop a network of social alliances more rapidly than young, socially naive males even in secondary transfers. Further, older resident males behave less aggressively toward young, newly transferred males than do males that are closer to the immigrant's age.

Pre-reproductive development of gender-specific patterns of behavior may be linked to species-typical reproductive tactics and life histories [45, 46]. It is important to take into account the developmental component in attempting to understand male migration. For baboons, male age is closely tied to dominance rank. There is a close correlation between age and rank among peers for juvenile males, with older juveniles dominating younger males and more generally with males outranking females. For juvenile males, dominance interactions probably serve to maximize access to food resources, which translates directly into growth and enhancement of competitive abilities. For females, dominance relations are a reflection of maternal dominance status. Recent work on the interactions of juvenile males and females with adults suggests that the males' social experience and access to high-quality nutrition may play a part in their 'choice' of reproductive tactics for adolescence and early adulthood [47, 48].

Whereas dispersal is widespread and most male baboons disperse at least once during their lives, evidence from several sites indicates that some males stay in their natal troop for a significant proportion of their lives, encompassing most, if not all, of their reproductive careers. Bercovitch [26] found that 4 of 12 adult males had remained in their natal group and accounted for most ejaculations in 40% of the consortships and that there was no

difference between natal and non-natal males in the proportion of mount attempts refused by females. In one instance, a male consorted with his sister, but she did not conceive during that cycle. At Amboseli, 'approximately 20% of the males reaching subadulthood or almost 30% of those reaching adulthood in Alto's group may have spent their entire reproductive careers there' [27]. This is in marked contrast to baboons in Gombe where 'it is likely that every male *P. anubis* ... transferred at least once during his lifetime and spent most of his reproductive life in a troop other than his natal troop' [19, p. 7]. The contrast between Amboseli and Gombe is possibly explained by the drastically different population densities at the two sites. Altmann and Altmann [49] report a home range of 24 km<sup>2</sup>, while at Gombe Packer [19] reports a home range size of 3.9–5.2 km<sup>2</sup>. On the other hand, only 1 male was observed not to leave his natal group (PIIG) at Gilgil with a group that exhibited a home range of over 70 km<sup>2</sup> [28]. Further, Bulger and Hamilton [36] in Botswana reported that 6 of 19 male chacma baboons were born into troops in which they later attained alpha status, and 3 of those males apparently sired at least 20 offspring. Paradoxically, home range size in their study group in the Okovango swamp is only 2.1–6.5 km<sup>2</sup> [50]. This suggests that the benefits of natal dispersal from the natal group may have been overestimated, at least under certain ecological and social conditions.

### **Affiliative Behavior and Dispersal**

Consort activity is not the only behavioral aspect of successful male dispersal. Several investigators have commented on the importance of greetings between males as a method males employ in forming long-term social relationships [51]. These greetings may be

viewed as a male's method of negotiating social relationships with other males that will later be important in competitive interactions. Manzotillo [28] noted that the frequency of greeting behavior increased twofold during the period of emigration into her study group. In particular, greetings between immigrants and residents increased significantly over expected values based on the number of immigrants and residents in the group. These accounts support Ransom's observation [31] that it is the immigrant that initiates the contacts with resident males.

In addition to mediating aggression received by newcomer males, females may directly influence male migration by the maintenance of nonconsort affiliations with males. Males that form fewer or less intense nonconsort bonds with females have a higher probability of emigration. Males that have the most intense and enduring social relationships with females also show the longest tenure in the group [26, 41]. It is important to recognize that the formation of social relationships with both resident male competitors as well as with noncycling females constitute fundamental challenges facing any successful immigrant baboon. Clearly, social strategies can ameliorate the costs associated with immigration, and males that negotiate these relationships are likely to become long-term group members.

### **Female Dispersal and Male Philopatry**

Recently, considerable attention has been directed toward female transfer [13, 24]. Although savanna-dwelling baboons are characterized by male transfer, mounting evidence indicates that female transfer also occurs at a variety of sites [summarized in 52], albeit much less frequently than for males. The reasons why individual females transfer are var-

ied [24], but under appropriate circumstances (small subgroups, low predation and reproductive failure), female baboons may actively seek to improve their reproductive status by transferring into another group [52]. The extent to which female transfer is governed by the same, or at least similar, proximate factors to male dispersal is at present unknown.

Nonetheless, the fact remains that under some circumstances females do leave their natal troop. Transfer has been noted for *P. cynocephalus anubis* [52], *P. cynocephalus cynocephalus* [38] and *P. cynocephalus ursinus* [52]. Anderson [52] notes that female baboons generally conform to Wrangham's model [42] of a female-bonded species and are generally not willing to forego the benefits of nepotistic group living. However, when troop size becomes small or troops regularly split into foraging parties, affiliation with relatives may confer fewer benefits. Females may actually accrue greater benefits by transferring to another group through obtaining access to novel mating partners or improved resources.

### **Summary**

The dispersal process is still poorly understood, in part because there have been few attempts to follow dispersing males from one troop to another [for notable exceptions, see 19, 40, 49]. A number of investigators have, however, commented on the process by which males enter new troops. The exact technique of entry into a troop and the latency to full integration, as measured by social and sexual affiliations, varies with age, experience, physical condition, personality and characteristics of the target group [30, 40, 49, 53]. Depending upon these factors, several alternative tactics appear to be available to males.

Although it can be argued that dispersal has been well documented for baboons, it is far from clear that we can identify all the proximate factors stimulating dispersal either from the natal group or from breeding groups. Moreover, we are largely ignorant about the factors that cause animals to choose one group rather

than another. However, there should be some cause for optimism precisely because baboons have been so thoroughly studied. A careful cost/benefit analysis of dispersal at a site that allows for frequent intertroop interactions and low male dispersal costs is likely to be informative about factors influencing male dispersal decisions. Moreover, in order to fully understand patterns of dispersal in *Papio*, we must attempt to understand the differences within and between study populations. Variations in key features of the dispersal process have been carefully documented at several sites, and it is important to identify the sources of this variation.

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