

# Why Vervet Monkeys 13 (*Cercopithecus aethiops*) Live in Multimale Groups

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## *Introduction*

Explanations of patterns of male residence in primate groups have long been sought by behavioral ecologists. The permanent co-existence of multiple males with groups of females is unusual in mammals, but primates include a large number of such species. In cercopithecine primates alone, 17 of 44 species (39%) live in multimale groups year-round (Smuts *et al.*, 1987). Suggested determinants of male residence patterns in primates include phylogenetic constraints (Struhsaker, 1969), female defensibility (numbers of females, or temporal and spatial distribution of females) (Clutton-Brock and Harvey, 1977; Wrangham, 1979, 1980; van Schaik and van Hooff, 1983; Terborgh, 1983; Andelman, 1986; Ridley, 1986; Dunbar, 1988; Altmann, 1990; Janson, 1992; Mitani *et al.*, 1996; Nunn, 1999), predation (Struhsaker, 1969; Crook, 1972; Henzi, 1988; van Schaik and van Noordwijk, 1989;

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Baldellou and Henzi, 1992; van Schaik and Hörstermann, 1994), cooperative defense of food (Isbell *et al.*, 1991) or females (Mitani *et al.*, 1996), and trade-offs between time spent in feeding and defense of females (Terborgh and Janson, 1986). None of these factors appears to account for the co-existence of multiple males in female groups of vervet monkeys (*Cercopithecus aethiops*). Vervet monkeys are exceptional not only among guenons, the majority of which have only one resident male in their groups year-round, but also among all primates, and alternative explanations for their multimale social organization must be sought. Here we briefly discuss why current hypotheses are not adequate for vervet monkeys and propose a new alternative hypothesis.

### *The Inadequacy of Current Explanations*

#### *Phylogenetic Constraints*

Cercopithecines show a phylogenetic pattern of male residence and female philopatry. In all species, females typically remain in their natal groups throughout life, whereas males typically disperse around sexual maturity. Savannah baboons (*Papio* spp.) and macaques (*Macaca* spp.) live in multimale groups throughout the year, whereas most guenons (*Cercopithecus* spp.) live in single-male groups outside the breeding season. Patas monkeys (*Erythrocebus patas*), which are so similar to other guenons that they are sometimes included in the genus *Cercopithecus* (Gautier-Hion *et al.*, 1988; Groves, 2001), display the typical guenon single-male social system (Chism and Rowell, 1988). Although phylogeny may play a role in behavioral differences between the Cercopithecini and Papionini in general, it cannot explain the multimale social organization of vervet monkeys, which are more closely related to other guenons than to baboons and macaques.

#### *Defensibility of Females*

Numerous studies indicate that male numbers in groups of primates are influenced by some quality of females, which could be the number of females in the group, the length of the breeding season, the degree of estrus synchrony, or the spatial spread of the females (Andelman, 1986; Ridley, 1986; Altmann, 1990; van Hooff and van Schaik, 1992; Mitani *et al.*, 1996; Nunn, 1999). In guenons such as patas monkeys, Schmidt's redtailed monkeys (*Cercopithecus ascanius schmidti*), and Stuhlmann's blue monkeys (*C. mitis stuhlmanni*), multiple males sometimes reside temporarily with larger groups of females during the breeding season (Cords, 1984, 2000; Cords *et al.*, 1986; Harding and Olson, 1986; Carlson and Isbell, 2001). Multimale influxes have never been reported outside of the breeding season, which suggests that

exclusion of other males is easier when there is no possibility of reproducing. In patas monkeys, the resident male actively excludes extragroup males throughout the year, sometimes fatally wounding them (Isbell, unpub. data). Why the resident male should bother to exclude other males outside the breeding season is puzzling, given that females cannot conceive then.

Vervet monkeys are similar to other guenons in numbers of females per group, length of the breeding season, numbers of females mating per day within groups, and group spreads (Table I). Vervet monkeys meet all the requirements for successful exclusion of extra males, and yet they are nearly always multimale, even outside the breeding season. Factors other than female defensibility must favor multiple males (Henzi, 1988), because vervet monkeys differ from other guenons most during the non-breeding season.

### *Predation*

Vervet monkeys live in savannah-woodlands, which are more open than forests, and carnivores are common in the savannah-woodlands. It has long been assumed that primates living in the more open habitats suffer higher predation rates than primates in more forested habitats (Altmann, 1974; Dunbar, 1988; Isbell, 1994; Olupot and Waser, 2001). Vervet monkeys can suffer high levels of predation (Cheney *et al.*, 1988; Isbell, 1990). Predation on vervet monkeys in Amboseli National Park, Kenya, the population for which predation is best documented, is mirrored by similarly high predation in vervet monkeys on Segera Ranch on the Laikipia Plateau, Kenya. Segera is a semi-arid savannah-woodland with an intact community of potential predators of primates, including leopards (*Panthera pardus*), lions (*P. leo*), black-backed jackals (*Canis mesomelas*), and martial eagles (*Polemaetus bellicosus*) (Isbell, 1998). Using the criteria of Cheney *et al.* (1988) and modified by Isbell (1990) for Amboseli vervet monkeys, Isbell and Enstam (2002) found, for example, that a minimum of 10 of 18 (56%) adult female vervet monkeys on Segera have died of suspected or confirmed predation.

In a population of vervet monkeys in South Africa, Baldellou and Henzi (1992) tested the hypothesis that predation could account for the vervet multimale social organization by determining whether males provide an advantage to females against predators. They found that although males were more vigilant than females, they were not better than females at detecting predators. In addition, the highest-ranking male was more vigilant and more active against predators than all other males. This led them to suggest that vervet monkey groups have multiple males because supernumerary males attach themselves to groups to minimize their own risk of predation.

If this hypothesis is correct, we would expect patas monkeys, which live in more open habitats and are more terrestrial than vervet monkeys, to live in permanent multimale, multifemale groups also, but they do not. Like vervet

**Table I. Traditional Factors that Affect Female Defensibility in Vervet Monkeys vs. Other Guenons**

Species, location	No. females in group	No. males in group on same day	Length of birth season	No. females mating per day	Group spread	Sources
Vervet monkeys, Amboseli	range: 1–8 ( <i>n</i> = 6 groups)	1–6 yr-round	3 months	mean: 1.8 range: 1–3	mean: 55 m ± 0.97 SE	Isbell, L. A., unpub. data
Vervet monkeys, Segera	2–4 (small group) 3–9 (large group)	1–3 (small group) 0–10 (large group) year-round	3–4 months		mean: 128.0 m ± 10.2 SE	Isbell and Enstam (2002)
Patas Monkeys, Segera	6–15 (one group)	1 outside breeding season; 0–6, breeding season	3–4 months	range: 0–7	mean: 151.8 m ± 6.8 SE	Enstam <i>et al.</i> , (2002); Isbell and Enstam (2002); Carlson and Isbell (2001)
Red-tailed Monkeys, Kibale	range: 5–16	1 outside breeding season; 1–6, breeding season	most, if not all, months		median: 51–55 m	Struhsaker and Leland (1979); Butynski (1988); Struhsaker (1988)
Red-tailed Monkeys, Kakamega	10	1 outside breeding season; 1–4, breeding season	6 months	maximum: 3	mean: 56 m range: 20–85 m	Cords (1984, 1987a,b)
Blue Monkeys, Kibale	mean: 4.5–10	mean: 1	most months		median: 46–50 m	Struhsaker and Leland (1979); Butynski (1988)
Blue Monkeys, Kakamega	range: 6–18	mean: 5.9; range: 2–11, breeding season	most months	mean: 3.8 range: 1–8	mean: 109 m range: 60–190 m	Cords (1986, 1987b)

monkeys, Segera patas monkeys also suffer high mortality, much of which is from predation. Of 34 adult female patas monkeys that died during the study, 16 (47%) died of suspected or confirmed predation. We were unable to determine the cause of disappearance for 12 adult females (35%) because we were often unable to find the group in their large home range within our three day window of opportunity for assigning disappearances to predation (Isbell and Young, in prep.). We may have underestimated predation.

Cords (2000) suggested that predation could still explain the differences between vervet monkeys and patas monkeys if male patas monkeys have different strategies for dealing with predators that enable them to avoid predation better than male vervet monkeys do. However, Enstam and Isbell (in press) found that when vervet monkeys and patas monkeys were in the same habitat, they responded similarly to alarm calls, i.e., in areas with short trees, they both fled on the ground and did not attempt to hide from predators.

### *Home Range Defense*

In vervet monkeys, male survival can depend on access to food resources (Wrangham, 1981) and male reproductive success appears to be influenced more by longevity than by dominance status (Cheney *et al.*, 1988). An examination of the dynamics of group disintegration and fusion in Amboseli revealed that adult males and adult females behaved similarly to maintain groups at the minimum group size of two adults regardless of the sex of the adults (Isbell *et al.*, 1991). Vervet monkeys are one of very few multimale, territorial species (Wrangham, 1980) and it has been suggested that male vervet monkeys benefit directly from home range defense (Isbell *et al.*, 1991). Cords (2000) has raised a counter-argument, however, that weakens the home range defense hypothesis: vervet monkeys exhibit substantial variation in the frequency or intensity of home range defense but this variation is not mirrored by the vervet monkey grouping pattern. In populations wherein home range defense is infrequent, vervet monkeys still live in multimale groups (Kavanagh, 1981; Cheney, 1987).

### *Cooperative Defense of Females*

Mitani *et al.* (1996) suggested that cooperative associations of males to defend females could help explain extra males in primate groups, i.e., groups that had too few females to account for the number of males in them. However, this does not explain the vervet multimale social system. Male vervet monkeys do not form coalitions within groups to defend access to females, and, of all males, the alpha male is most frequently involved in aggressive intergroup encounters (Cheney, 1981).

*Time Constraints*

Terborgh and Janson (1986) suggested that multimale groups could result if males are forced to make trade-offs between obtaining their food and defending females. Noting that frugivorous primates tend to live in multimale groups whereas folivorous primates tend to live in single-male groups, they suggested that this difference might exist because frugivorous species require more time for feeding or foraging, which reduces the time available for defending exclusive access to groups of females. However, this does not explain why the vervet social system differs from that of most other guenons. Though vervet monkeys are more frugivorous than folivorous, so are most guenon species that live in single-male groups (Cords, 1987a). More importantly, vervet, red-tailed, and blue monkeys all spend *ca.* 30% of time feeding (Struhsaker and Leland, 1979; Isbell and Young, 1993), and vervet monkeys spend less time foraging than patas monkeys do (Isbell *et al.*, 1998).

*An Alternative: The Limited Dispersal Hypothesis*

We suggest here an alternative hypothesis to account for the vervet multimale social system. The limited dispersal hypothesis proposes that two elements, configuration of the habitat and costs of dispersal, determine the number of groups available for a dispersing male to join. If the configuration of the habitat results in a small number of adjacent groups and the costs of dispersal are high, dispersing males limit their movements to adjacent groups and do not transfer often in their lifetimes. Immigrant males refrain from committing infanticide in the groups they join because they are sufficiently related genetically to members of their new groups that committing infanticide would decrease their inclusive fitness. Multimale groups form because the minimal risk of infanticide also favors tolerance of immigrant males by group members. However, as the configuration of the habitat allows groups to share borders with a greater number of adjacent groups and the costs of dispersal decrease, it becomes increasingly likely that dispersing males will join groups without relatives. Such males will be more likely to attempt infanticide and members of groups will be less tolerant of them, even to the point of excluding them. The vervet social system should be facultatively multimale because habitat configuration and costs of dispersal are dependent on local environmental conditions.

Vervet monkeys typically live within narrow belts of vegetation along rivers (Wolfheim, 1983). Adjacent to them are drier, more sparsely treed habitats, which are unsuitable for vervet monkeys. A vervet monkey group is usually bordered by two groups, one at either end of its linear home range. There are exceptions, of course, the best known being Amboseli, where

vervet monkeys lived along swamps rather than rivers (Cheney *et al.*, 1988). The less restricted configuration of the habitat in Amboseli enabled up to five groups to border the home ranges of each group (Cheney and Seyfarth, 1983). Unprovisioned vervet monkeys nearly always live near water, which limits their distribution in savannah-woodlands.

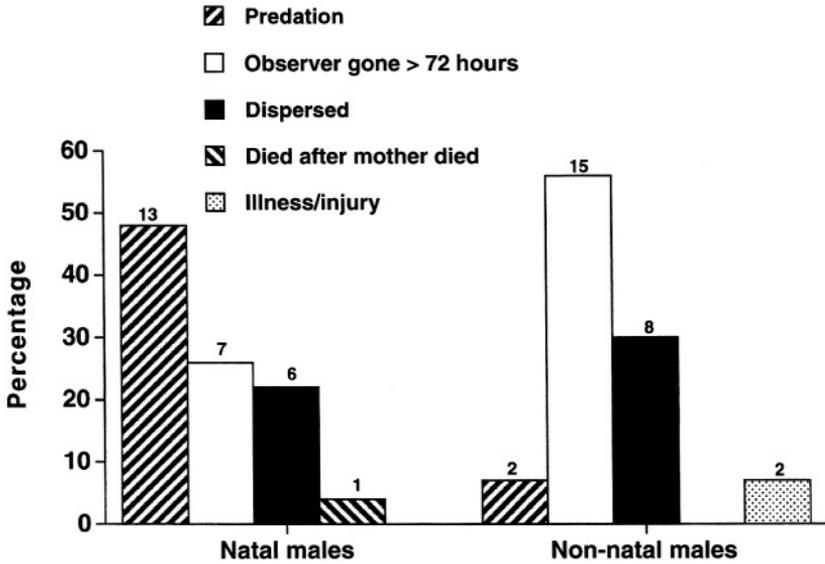
Dispersers often face higher risks of mortality than philopatric animals (Shields, 1982; Isbell *et al.*, 1990, 1993; Alberts and Altmann, 1995; Olupot and Waser, 2001). Dispersal costs are difficult to estimate, however, because individuals that disappear may have emigrated to distant groups or died. That dispersal can be costly to male vervet monkeys is suggested by greater mortality of female and immature vervet monkeys when they moved into unfamiliar areas (Isbell *et al.*, 1990, 1993). Because vervet groups have little home range overlap, dispersal typically involves moving into unfamiliar areas.

### *Segera Vervet Monkeys*

The vervet monkeys on Segera are typical of ones elsewhere in Africa. No Segera vervet monkey group lives in a home range without access to a river. Home ranges are small (10–40 ha), linear, and contiguous, and when population density is sufficiently high, they occupy all habitat along the rivers. Outside the home ranges, there is no suitable habitat. Since the long-term study began in 1992, we saw a vervet monkey only once *ca.* 2 km from a river. Each vervet monkey group is bordered by two adjacent groups, one on either end of its linear home range.

Few Segera males survive long enough in their natal groups to disperse, but those that do typically emigrate to either of two adjacent groups. Of 27 males either born into two Segera study groups or not yet fully grown at the beginning of the study, 21 (78%) either died ( $n = 14$ ) or disappeared ( $n = 7$ ) (Fig. 1). Because four that disappeared were one to six months old and too young to transfer, they presumably died. The other three were five to six years old and could have transferred to non-adjacent groups, though we did not see them in those groups. Six males (22%) survived to disperse, and stayed an average of 16 months in the new groups. Five of them (83%) transferred to adjacent groups. Two were maternal brothers that transferred into the same group one year apart. Thus, even with high mortality, closely related males can disperse into the same group.

We also monitored the movements of 27 non-natal males. Four died before they could transfer again (Fig. 1). Fifteen (56%) are unexplained disappearances. The high percentage of disappearances of non-natal males relative to natal males suggests that some of them could have transferred to non-adjacent groups, though we did not see them there. Eight non-natal males (30%) transferred again, and all of them moved to adjacent groups. Including movements into the study groups, one transferred  $\geq 3$  times,



**Fig. 1.** Fates of natal and non-natal male vervet monkeys on Segera Ranch, Laikipia, Kenya, over a nine-year period. Suspected and confirmed predation were included in the category of predation.

with  $\geq 2$  of the transfers in the same direction. Four males transferred at least twice. The average length of tenure for non-natal males was 20 months ( $n = 28$  transfer events).

As Cheney and Seyfarth (1983) have pointed out for Amboseli vervet monkeys, the effect of such non-random dispersal is that males are genetically more closely related to members of the groups that they join than if dispersal were random. We further suggest that because male vervet monkeys typically have fewer dispersal options than other species, they are also genetically more closely related to members of their new groups than are dispersing males of other species.

Not only might maternal brothers disperse into the same group but also their fathers might have dispersed into the same group before them, and reproduced. Consider the following scenario: a male transfers into Group 1 during the breeding season. He fathers a son in that group, stays for 20 months, and then transfers to adjacent Group 2. In Group 2, the male fathers a daughter and a son. By the time his daughter is reproductively mature (at four years; Cheney *et al.*, 1988), his son from Group 1 is five to six years old and ready to transfer. If his son transfers to Group 2 (a high probability since there are only two groups available), he will have two paternal sibs in the new group, one of which is a potential mate.

Limited dispersal should favor mutual tolerance by increasing the average degree of relatedness between immigrants and their new groupmates.

Immigrant males would be expected to be more tolerant of the offspring of other males, including unweaned offspring. Immigrants would not commit infanticide because doing so would decrease their inclusive fitness. Resident males and females would be expected to be more tolerant of non-group males, even to the extent that they are allowed into the groups, because these males are related and will not attempt to commit infanticide. Indeed, no suspected or confirmed infanticides by immigrant males have occurred on Segera over nine years and 58 births and 20 immigrations.

Dispersal to adjacent home ranges by both natal and non-natal males and dispersal of siblings to the same group on Segera are remarkably consistent with those from Amboseli (Cheney and Seyfarth, 1983). In Amboseli, where swamps enabled more vervet monkey groups to share home range borders than is possible along rivers, males from the same natal group tended to restrict their movements to a subset of the groups available to them. Similarly, Henzi and Lucas (1980) reported dispersal to adjacent groups and joint dispersal by males in a provisioned population in South Africa. Limiting dispersal to adjacent groups may help males mitigate the high costs of dispersal (Pusey and Packer, 1987; Isbell and Van Vuren, 1996). Although males in other species also disperse to adjacent groups, sometimes with siblings (Pusey and Packer, 1987), vervet monkeys appear to differ from other primates in having a more limited number of adjacent groups into which dispersing males can go.

In Amboseli, where the number of adjacent groups was higher for each group than at Segera, the estimated rate of infanticide was also higher. Infanticide by immigrant males was suspected in the deaths of three of 148 infants (2%) during 66 immigration events over 11 years. The estimated infanticide rate, weighted by the number of births and immigration events, was 0.03 infanticides per 100 immigration events (three infanticides/148 births)/66 immigration events  $\times 100$ ). We suggest that the absence of infanticide of vervet monkeys on Segera results from their living along a river in a habitat, where dispersal costs are high, which limits dispersal options to one of two groups, whereas Amboseli vervet monkeys' higher infanticide rate is a result of their living around swamps, which provided more options for dispersal into adjacent groups. Nonetheless, the rate of infanticide in Amboseli was still quite low, which may be a consequence of the tendency of natal groupmates to disperse to the same groups.

### *Testing the Limited Dispersal Hypothesis*

The limited dispersal hypothesis predicts that the vervet multimale social system is facultative and dependent upon the costs of dispersal and the configuration of the habitat. If limited dispersal minimizes the risk of infanticide so that exclusion of other males is possible but not necessary, then

less limited dispersal should increase the risk of infanticide and, at some point, make exclusion necessary. This prediction is supported by the behavior of vervet monkeys in Barbados.

Barbados vervet monkeys are relatively evenly distributed, with opportunities for gene flow throughout the island (Horrocks, 1984). In addition, because their only predators are humans and domestic dogs and they feed extensively on cultivated food (Horrocks and Hunte, 1986) the costs of dispersal appear to be relatively low. This suggests that dispersal options are greater for Barbados vervet monkeys than for vervet monkeys on Segera and in Amboseli. Barbados vervet monkeys usually live in single-male groups (Horrocks and Hunte, 1986). As in other species with single-male groups, extragroup males and aggressive takeovers occur in the population (Horrocks and Baulu, 1988). Horrocks (1986) suspected infanticide in the deaths of two of 22 (9%) infants during two immigration events. Infanticide appears to be a serious cause of infant mortality (Horrocks and Baulu, 1988). The estimated infanticide rate among Barbados vervet monkeys is 4.5 infanticides per 100 immigration events. Detailed information on dispersal distance, time spent as an extragroup male, likelihood of becoming a resident male, and tenure with female groups would help to clarify the effect of dispersal on behavioral differences between males living in single-male and multimale populations of vervet monkeys.

Single-male groups also occur in Naivasha, Kenya. Turner *et al.* (2001) collected genetic material from them as well as from populations with multimale groups. Accordingly, it should be possible to test the limited dispersal hypothesis via genetic analyses. It would also be useful to compare vervet monkeys in single-male and multimale populations with other guenons. Like vervet monkeys that live in single-male groups, other guenons in single-male groups are predicted to have a lower degree of relatedness between immigrant males and the groups they join than vervet monkeys that live in multimale groups.

### *Dispersal Options and Infanticide in Other Guenons*

Unlike most vervet monkeys, forest guenons and patas monkeys live in home ranges surrounded by additional suitable habitat that could be used by multiple groups. Male forest guenons and patas monkeys are thus likely to have more groups into which they might disperse. We expect immigrant male forest guenons and patas monkeys to be much less genetically related to the members of their new groups than vervet monkeys living in multi-male groups. Consequently, we also expect immigrant male forest guenons and patas monkeys to attempt infanticide more often than immigrant male vervet monkeys in multimale groups.

Infanticide has been strongly suspected or directly observed in Stuhlmann's blue monkeys, Schmidt's red-tailed monkeys, Lowe's monkeys (*Cercopithecus campbelli lowei*), and patas monkeys (Struhsaker, 1977; Galat-Luong and Galat, 1979; Butynski, 1982; Enstam *et al.*, 2002). It appears to be rare in patas monkeys because males that are present for the birth season were also usually present during the previous breeding season and thus are potential fathers. In a case in which a male became resident after the breeding season and stayed for the next birth season, he attacked an infant, which we found dead five days later. Bite wounds on its body, female behavior toward the male, and the male's behavior before and after the infant's death indicated that he caused the death. If we view infanticide as an extreme form of male–male competition rather than a male strategy against females, it becomes much easier to reconcile the occurrence of infanticide in species that were not originally expected to have infanticide, i.e., multimale species such as baboons (*Papio ursinus*; Palombit *et al.*, 2000) and seasonally breeding species such as patas monkeys. We suggest that for guenons living in single-male groups, the resident male stays with the group outside the breeding season not to defend access to the females but instead to protect his putative infant offspring from infanticidal males.

### *Summary*

Although the presence of either one male or multiple males in primate groups appears in general to be a function of the number of adult females in those groups, vervet monkeys are an exception to this pattern. Given the small number of adult females per group, one would expect vervet monkey groups to have only one adult male, but instead they typically have multiple adult males. Several other possible determinants of multimale social organizations have been proposed, including compressed temporal distribution of estrous females, large group spread, heavy predation, phylogenetic history, and feeding constraints. We discussed and dismissed each of these for vervet monkeys, and provided an alternative hypothesis. The limited dispersal hypothesis proposes that habitat configuration and costs of dispersal favor multimale groups of vervet monkeys by limiting dispersal options for males. Limited dispersal options increase the genetic relatedness between immigrants and members of their new groups, which selects against infanticidal behavior by immigrant males. Exclusion of immigrant males thus becomes unnecessary, resulting in multimale groups. We provided nine years of demographic data on male vervet monkeys of Segera Ranch, Kenya, as an example of a vervet monkey population with limited dispersal options. Comparison of infanticide rates of Segera vervet monkeys with those of vervet monkey populations having greater dispersal options provided support for the hypothesis. Multimale groups of vervet monkeys appear to be facultative responses to local

environmental conditions that affect dispersal options. A similar comparison of multimale vervet monkeys with single-male forest guenons and patas monkeys led us to suggest that in these species the resident male remains with females outside the breeding season not to defend females but to defend his putative offspring from infanticidal males.

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