

# When are there Influxes 14 in Blue Monkey Groups?

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## *Introduction*

An enduring question in behavioral studies of group-living primates is what determines the number of males in a group (Kappeler, 2000). Variation in male number occurs on several scales: there may be persistent differences among species, among populations or groups of single species, and even within single groups over time. The variables that explain variation on these different scales are not necessarily the same (Henzi, 1988).

I discuss factors that explain variation within single groups over time in forest-dwelling blue monkeys (*Cercopithecus mitis*). Like most other forest guenons, as well as closely related patas monkeys (*Erythrocebus patas*), blue monkey groups include only one adult male most of the time, especially outside the breeding season. During the breeding season, however, the number of males in a group of blue monkeys, and in some other guenon species, is more variable (Cords, 1987a, 1988, 2000; González-Martinez, 1998; Kaplin *et al.*, 1998; Macleod, 2000). Studies of blue monkeys, redtailed monkeys (*Cercopithecus ascanius*) and patas monkeys have revealed how the one-male group persists during some breeding seasons: the male that has been with the females previously continues to accompany them, and is the only male continuously present. Other males may make occasional, brief visits, but they do not remain

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in the group. In blue and patas monkeys, most male visitors are known to be non-resident in any heterosexual group, but a few are residents from neighboring groups, which typically make their visits at territorial boundaries or during intergroup encounters. At the other extreme are breeding seasons in which the one-male group structure breaks down completely and several adult males come into the group, often for longer periods, as part of a multimale influx (Cords, 1988). Prior residents may be ousted during an influx, or they may weather influxes and persist as the sole resident when breeding subsides.

While intermediate cases exist, it seems legitimate to dichotomize breeding periods into influx and non-influx years. For the Kakamega blue monkey population, there is no overlap in the values of distinguishing criteria. Specifically, during influx years there is a more conspicuous and continuous presence of multiple males (50–94% of days in six influx seasons vs. 4–28% of days in ten non-influx seasons), and both the average number of males per day (1.6–3.8 in an influx, 1.0–1.3 in a non-influx year) and the maximum number of males per day (11 in an influx, four in a non-influx year) are higher than in non-influx years (Cords, 2000, with additional data from 1998–2001). The duration of the typical male visit also differs, lasting days or weeks in influx years, but only a few hours in non-influx years.

My goal is to explain variation in the occurrence of multimale influxes. Using long-term data from 23 years of monitoring breeding seasons in one blue monkey population and detailed records of the behavior of individually identified males and females in two to four study groups over seven years, I examine correlates of influx breeding seasons. I predicted that influxes should be most likely when a resident male's ability to exclude other males is low. Indeed, blue monkey males behave as if they want to keep other males away from their females, being highly vigilant—seemingly toward rivals, rather than predators—and likely to chase intruding rivals if detected. However, intruders appear to be attracted to groups that offer reproductive opportunities, and they often copulate with females that may prefer them as mates. When many females are mating, it should be especially difficult for residents to exclude other males, and more likely that multiple males are present.

Female blue monkeys are not necessarily fertile (ovulating, non-pregnant) when they mate (Pazol *et al.*, 2002). While it might benefit males to distinguish fertile from infertile females, there is no evidence that they do so. Female blue monkeys do not have external signs of fertility, and olfactory signals also seem poorly developed (males rarely sniff females). Therefore I assume that female mating behavior, i.e., estrus, is the best indicator of reproductive opportunities available to males.

### *Methods*

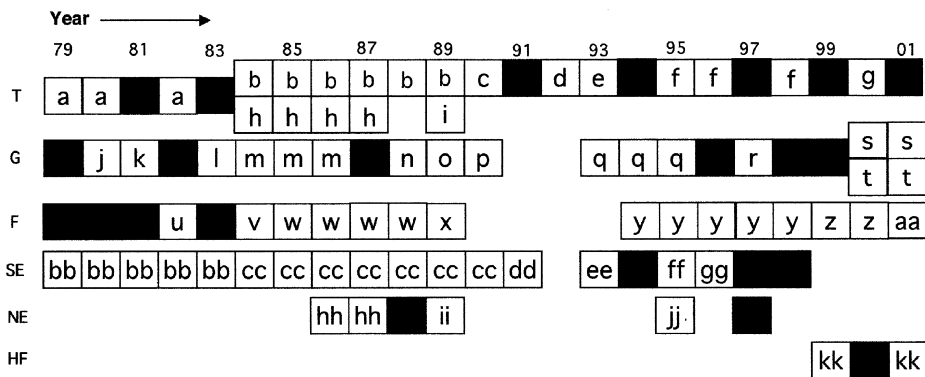
I studied blue monkeys (*Cercopithecus mitis stuhlmanni*) inhabiting the Kakamega Forest, western Kenya (Cords, 1987b). This rain forest fragment,

whose main block is approximately 86 km<sup>2</sup> (Brooks *et al.*, 1999) at about 1650 m, receives an average annual rainfall of >2000 mm. Two rainy and two dry seasons per year can usually be distinguished, but there is much interannual variation.

Kakamega blue monkeys occur at a density of *ca.* 170–220 individuals/km<sup>2</sup> (Cords, 1987b; Fashing and Cords, 2000), with the higher figures more representative of the periods in the last eight years when reproductive behavior was most intensively sampled. This is a high population density for the species.

Several groups have been monitored to various degrees since 1979 and provide general information on the occurrence of multimale influxes (Fig. 1). The two main study groups, T and G, have been followed on a nearly daily basis during most of the breeding season since 1979 and 1994, respectively. Both have fissioned within this period, T in 1984 and G in 1999. Monitoring of Te, one of the daughter groups of the original T group, lasted only until 1989, after which a change in ranging patterns prevented continued contact. Tw, the other daughter group, has been monitored through the present. Both daughter groups of G (Gn and Gs) have been monitored since they separated from each other in 1999.

The most detailed records on male presence and sexual behavior are available from Tw, G, Gn and Gs groups from 1995 to 2001, when each was followed daily through the breeding season by a team of two to three observers. During this period of intensive monitoring, we aimed to keep



**Fig. 1.** Males present in study groups of blue monkeys during the 1979–2001 breeding seasons. Each row represents one group, two of which fissioned (T in early 1984, G in late 1999). Each box represents a particular breeding season for a given group in a given year. Letters are used to designate the identity of individual resident males in non-influx years; black-shaded boxes represent multimale influx years. If no box is present for a particular year, the group was not monitored thoroughly enough to determine the number of males present.

continuous contact with sexually active adults, and regularly patrolled the group's periphery searching for intruding males. In earlier years with less intensive observations, we also recorded which females mated and which had infants the following breeding season. Before 1998, some conceptions may have been missed if an infant was born and died during gaps in observations, which were limited to the breeding season.

Information on the frequency of multimale influxes is also available for four additional groups in the population, all of which are neighbors of the main study groups. They were followed intermittently and opportunistically to determine how many and which males were present during the breeding season.

All adult males and females in the T and G groups were individually recognized using natural characteristics. In the neighboring groups, only the adult males were individually recognized. Adult males typically have more distinctive characteristics than females and juveniles, including scars, stiff or missing digits, and distinctive pyow vocalizations. In T and G groups, female parity was estimated based on nipple elongation early in the study, and was known from longitudinal records later on.

Some of the analyses required a distinction between sexually active (estrous) and inactive females. A female is considered estrous on a given day or in a given season if she mated or puckered to a male from  $\leq 2$  m away. Puckering is a proceptive behavior that female blue monkeys direct toward males, and it does not occur in any other social context. Most puckering females mated at, or close to, the time when they puckered. Female blue monkeys use other signals of proceptivity, such as presenting the hindquarters and head-flagging, but they also occur in non-sexual contexts, so were not useful to describe estrus unambiguously.

For data analysis, a mating season is the period from June 15–October 31. Sexual behavior was absent or sporadic in the weeks before and after this period. Records of male presence and female sexual activity from 1995–2001 span this period in every group and year, except for G in 1999, when the mating season ended on October 4. This was the date when G fissioned permanently into Gn and Gs. For October 5–31, I did not combine data from the two daughter groups with those from the original G group because of the enormous change in the social milieu. In comparisons of influx and non-influx mating seasons, I report mean values and associated standard errors of several variables.

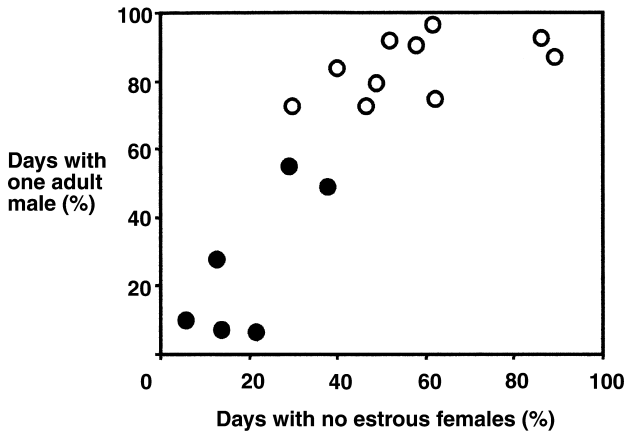
## *Results*

Multimale influxes have occurred in all the groups that we have monitored at Kakamega (Fig. 1). Overall, they occurred in 23% (23/98 group-years) of breeding seasons. The frequency of influxes per group varies

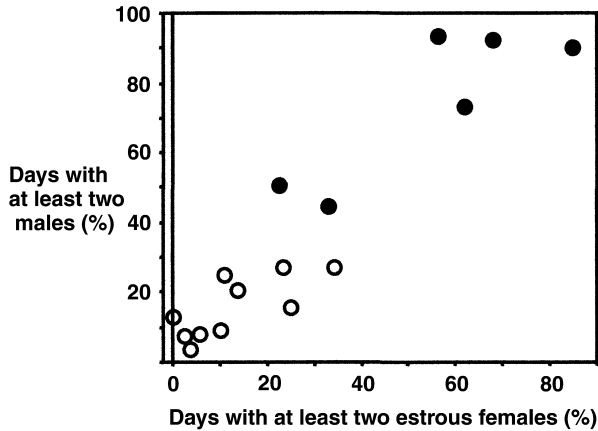
from 0 to 40% ( $n = 10$  groups, with fission products being considered separately from the parent group). It is mainly during the breeding season that multiple males are in the group. When breeding subsides, all but one male leave the group. In only one of 14 group-years of year-round monitoring of our main study groups did we find multiple males in a group for several months after mating activity had subsided.

The number of potentially fertile females in a given year included parous females without young and ones whose most recent offspring were  $\geq 12$  months old, given that interbirth intervals in the population are  $\geq 2$  years when the first offspring survives (Cords and Rowell, 1987). Nulliparous females that mated were also included as potentially fertile. The number of potentially fertile females was higher during influx years ( $\bar{x} = 13.4 \pm 1.5$ ,  $n = 10$ ) than during non-influx years ( $\bar{x} = 9.6$ ,  $\pm 0.5$ ,  $n = 24$  years; Mann Whitney U Test,  $p = 0.024$ ). There were even bigger differences in the number of females that actually mated in influx ( $\bar{x} = 12.4 \pm 1.7$ ,  $n = 10$ ) and non-influx years ( $\bar{x} = 6.9 \pm 0.6$ ,  $n = 24$ ; Mann Whitney U Test,  $p = 0.005$ ).

From the viewpoint of individual male behavior, these seasonal figures may be less relevant than what is happening on individual days within a given season. In non-influx years, there were more days with no female in estrus ( $\bar{x} = 57.4 \pm 5.9\%$  of days,  $n = 10$  seasons) than in influx years ( $\bar{x} = 20.1 \pm 4.8\%$  of days,  $n = 6$  seasons; Mann Whitney U Test,  $p < 0.002$ , Fig. 2). Across all 16 breeding seasons, there were many days with just one male in the group when there were also many days with no estrous female in the group ( $r_s = 0.86$ ,  $p < 0.001$ , Fig. 2).



**Fig. 2.** The number of males in the group as a function of the presence of estrous females. Each data point represents one breeding season in one group. Solid points are influx seasons, while open points are non-influx seasons. Data come from Tw (1995–2001), G (1995–1999), Gn and Gs (2000–2001).

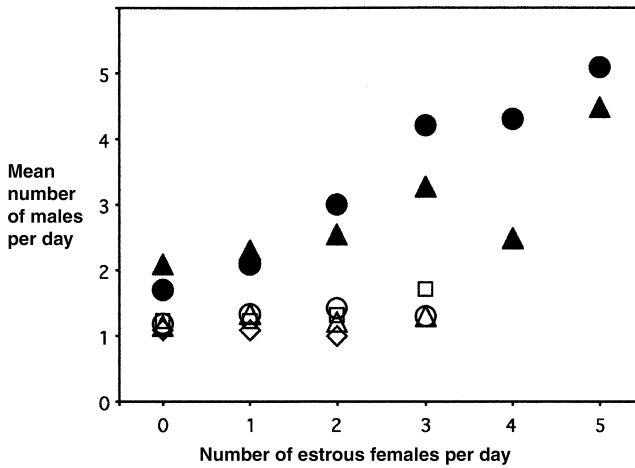


**Fig. 3.** The number of males in the group as a function of the prevalence of estrus synchrony. Each data point represents one breeding season in one group. Solid points are influx seasons, while open points are non-influx seasons. Data come from Tw (1995–2001), G (1995–1999), Gn and Gs (2000–2001).

Estrus synchrony—two or more females in estrus on a given day—was also more likely to occur during influx ( $\bar{x} = 54.5 \pm 9.4\%$  of days,  $n = 6$  years) than non-influx years ( $\bar{x} = 12.9 \pm 3.5\%$  of days,  $n = 10$  years; Mann Whitney U Test,  $p < 0.005$ , Fig. 3). Across all breeding seasons, the frequent presence of  $\geq 2$  females in estrus coincided with the frequent presence of  $>1$  male in a group (Fig. 3,  $r_s = 0.88$ ,  $p < 0.001$ ).

If the presence of multiple estrous females makes successful exclusion of other males difficult, one might also expect to see a relationship between the number of males and the number of estrous females on a day-to-day basis. During influx years, there were indeed more males in the group on days when more females were estrous (Fig. 4; Jonckheere Test for Ordered Alternatives,  $p < 0.00003$  for Tw and for G groups). During non-influx years, the relationship between the daily number of estrous females and males in the group was less strong (Fig. 4; Jonckheere Test,  $p = 0.002$  for Tw,  $p = 0.063$  for G,  $p = 0.0007$  for Gs,  $p = 0.348$  for Gn).

The results presented so far show on various time scales that there is an association between the number of males and number of sexually active females in a group, but such an association does not clarify the direction of the causal arrow. Does female estrus bring males into the group, as the defensibility hypothesis suggests, or does the presence of males in the group bring females into estrus? There is evidence from Kakamega that male presence could stimulate estrus in females: in G, a resident male died outside the breeding season in 1998. He was replaced immediately by a succession of two males, and within three weeks of his death, nearly every female without a suckling infant



**Fig. 4.** The mean number of males in the group per day as a function of the number of estrous females present on that day. Data are combined over multiple seasons, with circles representing Tw, triangles representing G, diamonds representing Gn and squares representing Gs. Filled symbols show values for influx breeding seasons (1997, 1999, 2001 in Tw, 1996 and 1998, 1999 in G), while open symbols show values for non-influx seasons (1995, 1996, 1998, 2000 in Tw, 1995, 1997 in G, and 2000, 2001 in Gn and Gs).

began to mate (Pazol and Ziegler, 2000). Because this mating occurred in February and March, it seemed clear that the changed social situation, i.e., presence of new males, triggered the females' sexual behavior out of season.

In principle, observational data on male influx seasons can shed light on how female estrus and male numbers relate causally. If one thing causes the other, it should come first in time. Data are available for four influx seasons in which daily or near-daily observations of the study groups were made for  $\geq 6$  months before the onset of the breeding season. In two influx years (Tw 1999, G 1999), female estrus and the presence of additional males coincided very closely in time, and it is not possible to say with confidence which preceded which. In the G 1998 influx year, female estrus during the breeding season preceded the arrival of the first extra male by several weeks. In the Tw 2001 influx year, however, the presence of new males in the group preceded the first female estrus by about two weeks. These results are clearly not conclusive.

We can expand the sample size by considering non-influx years as well, since additional males usually turned up in the group during such years, even if their numbers were smaller and their stays shorter. Six non-influx seasons occurred in which intensive observations of the study groups preceded the advent of the mating season by many months. In five cases, some females became sexually active  $\geq 2$ –3 weeks before any additional males visited the group, while in the sixth case, female estrus and visits by males coincided

too closely in time to determine confidently which came first. Altogether, female estrus clearly preceded the arrival of male visitors in six breeding seasons, male visits preceded female estrus in one, and it is unclear whether estrus or male presence came first in the three remaining seasons.

### *Discussion*

Data from Kakamega blue monkeys support the hypothesis that variation in male numbers is related to defensibility of females. When more females are sexually active, whether over an entire breeding season or on a single day, there are likely to be more males in the group. From the standpoint of the behavior of individual males and females, this pattern makes sense. Males often guard estrous females by following them closely, and chasing or threatening rivals. Because females are widely spaced (Cords, 2002), a single male often cannot guard more than one of them. Even when only one female is estrous, intruding males can gain access to her if a resident temporarily moves away to feed or to investigate the presence of other intruders in another part of the group, which can be spread out over 300 m. The dense foliage of the forest environment means that wide interindividual dispersion goes hand in hand with limited visibility, and over the years we have witnessed many situations in which intruding males behave exactly as if they were taking advantage of an opportunity to sneak copulations undetected by a resident. The facts that intruding males mate with females and that influxes coincide with the breeding season underscore the importance of the defensibility of estrous females in influencing male numbers in a group. This analysis thus confirms conclusions derived from similar analyses of a subset of the data (Cords, 2000).

In a previous analysis (Cords, 2000), the question of whether female estrus brought males into the group or the presence of extra males brought females into estrus was not resolved. With supplementary data, it seems clear that male numbers do, at least sometimes, respond to sexual behavior of females. Such a mechanism must be in place if the female defensibility hypothesis is correct. The existence of such a mechanism does not, however, preclude a stimulating effect of male presence on female estrus. I suspect that both mechanisms operate synergistically in blue monkeys: the presence of males stimulates female sexual activity which in turn ensures the repeated arrival of new males during an influx season.

The importance of female defensibility is supported by comparative data across five populations of *Cercopithecus mitis*. The occurrence of influx breeding seasons in a population is related to the ratio of non-resident males to groups of females (Cords, 2000; Macleod, 2000). Influxes occur in populations wherein this ratio is at least one, but have not been reported in populations in which the ratio is less than one. The ratio of males to female-groups is a measure

of intruder pressure, and is independent of population density and sex ratio. Thus cross-population comparisons highlight another aspect of female defensibility that helps to explain variation in male numbers in blue monkeys.

Variable intruder pressure may be the factor that explains why the number of males in a group per day increases much more dramatically with the number of estrous females in the group per day in influx vs. non-influx years (Fig. 4). During non-influx breeding seasons, it appears that there are fewer males around the home range of the focal group, so fewer males may be available to move into groups when opportunity arises, when females are sexually active. During all breeding seasons, we make a point of regularly surveying the home ranges of the study groups and those of neighboring groups for adult males. During influx years, we routinely detected males during the surveys, but during non-influx years, they are harder to find. In thick vegetation, detecting non-resident, often solitary males, whose behavior is probably designed to be inconspicuous, is never an easy task, and would make quantitative estimates of their abundance extremely difficult. From a comparative perspective, however, I am confident that there are differences between influx and non-influx years. Studies of other guenon species, particularly red-tailed monkeys (Jones and Bush, 1988) and patas monkeys (Chism and Rogers, 1997), underscore the importance of variable male densities in facilitating multimale influxes.

If intruder pressure is an important component of female defensibility (along with the number of estrous females), and hence a cause of variation in male numbers in blue monkey groups, the question remains as to what factors bring about variation in intruder pressure. Across populations, demographic factors related to male mortality are likely to be important, as well as ecological factors that influence the size, and consequently the density, of female groups. What causes variable male density across local areas or between years in one site is unknown. Further study that focuses on non-resident male behavior is needed. Jones and Bush's (1988) study of radio-collared male red-tailed monkeys is a first step in this direction. As in Kakamega, they found that the density of non-resident males varied on a local spatial scale, and from year to year within the home range of a single group; however, their sample of individual males is too small to allow an understanding of this variation.

Data from other guenon populations and species, while less extensive, generally support my conclusions. Four groups of samango monkeys (*Cercopithecus mitis labiatus*) in Cape Vidal, South Africa, showed multimale influxes in one year, but non-influx breeding in the next year, when fewer females were receptive (Henzi and Lawes, 1987, 1988). In a later study of the same population, Macleod (2000) found that the number of males present on a single day in one group was correlated with the number of proceptive females on the same day. Among five red-tailed monkey groups in the Kibale Forest, Uganda, the number of adult females per group was negatively correlated with the proportion of time the group had only one adult male, and positively

correlated with the number of males seen in the group per observation month over a period of about 2–6 years (Struhsaker, 1988). In two patas monkey groups with adjoining ranges, influxes occurred less often in the group with fewer adult females (Chism and Rowell, 1986; Chism and Rogers, 1997). In one of them in another year, Harding and Olson (1986, their Fig. 2) showed that the number of males in the group on a given day was correlated with the number of sexually receptive females ( $r_s = 0.79$ ,  $n = 23$  days,  $p = 0.0002$ ). All these data point to the importance of the number of (receptive) females in determining how many males are in a group.

There are also reports that dispute the importance of female numbers in determining male numbers. In a two-year study of three groups of samango monkeys in the same population previously studied by Henzi and Lawes (1988), Macleod (2000) found that the mean number of males in a group during a single breeding season was not correlated with the number of potentially fertile females as defined by Cords (2000). Similarly, Jones and Bush (1988) found that the frequency of sightings of non-resident males during a breeding season was not related to the number of potentially fertile females in three groups of Kibale red-tailed monkeys. Harding and Olson (1986) noted that influx breeding seasons occurred in patas monkey groups that differed greatly in size.

While these reports may suggest that factors other than the number of receptive females can influence male numbers, it is also possible that measurements of reproductive opportunity were inaccurate. Across all existing studies of male influxes in guenons, the number of males in a group shows the closest relationship to the number of sexually active females per day, whereas measurements of reproductive opportunity that represent a group over an entire season predict male numbers less well. This fact probably reflects the proximate mechanisms that underlie a connection between female availability and male numbers: males seem to join groups in response to the behavior, not simply the number, of females that they detect.

Data from two other guenon populations also suggest that female receptivity determines the number of males in the group rather than vice versa. Henzi and Lawes (1988) seem to have simply assumed this causal direction for the Cape Vidal samango monkeys, perhaps because the reduction in female receptivity from one year to the next was largely related to the presence of young infants born to many of the group's females, thus removing them from the pool of possible mates. Macleod's (2000) follow-up study included more detailed monitoring of the chronology of female sexual behavior and males entering groups, and demonstrated for one group in one (influx) year that female proceptivity preceded males entering the group. Similarly, Harding and Olson (1986) found that males entered the groups a few days after females became sexually receptive, and that increases in the number of receptive females tend to precede increases in the number of intruding males. However, they do not comment on the events that occurred in the weeks before the influx

of males, and before the first female became receptive, so it is unclear whether observations began early enough in the season to allow a confident conclusion about whether female receptivity or male intrusions occurred first. However, they described how non-resident male patas monkeys monitor heterosexual groups, apparently looking for proceptive behavior in females; such behavior on the part of males would explain how their numbers respond to the presence of receptive females.

The importance of intruder pressure has been recognized by other researchers who focused on single populations (Struhsaker, 1988; Chism and Rogers, 1997). Only the work on samango monkeys, however, can address the relative importance of intruder pressure and number of receptive females to determine male numbers. Henzi and Lawes (1988) found an almost equal number of non-resident males that remained regularly around their study area in a year with influx breeding and in a year without influxes. While potential intruders thus seemed to be similarly available in both years, they spent more time with females in the year when more females were receptive. Further, Macleod (2000) noted that despite a similar availability of potential intruder males across groups in a single year, influxes occurred only in groups in which females were proceptive to non-residents. Accordingly, in samangos monkeys variable intruder pressure does not seem to explain as well as female behavior why influxes occur in only some groups and some years. It will be a challenge for future researchers of other populations to investigate further the importance of intruder pressure, a variable that is very difficult to measure under most field conditions (Struhsaker, 1988). If realized intruder pressure depends not only on the number of males but also on individual characteristics of particular residents, as suggested by Cords (1984), Struhsaker (1988), and Macleod (2000), documenting the importance of this aspect of female defensibility will be even more difficult.

### *Summary*

*Cercopithecus mitis* groups show variation in male number during the breeding season. The 23 years of male residence records from multiple groups of blue monkeys in the Kakamega Forest reveal that influxes occurred in 23% of breeding seasons, and coincide with greater number of sexually active females in the group on both per-season and per-day bases. In six of ten seasons with sufficiently detailed records, female sexual behavior preceded the arrival of multiple males in the group, while in one year, male visits came first, and in the remaining three years, estrus and the presence of more than one male occurred essentially simultaneously. It is likely that estrous females bring males to the group, but also that the presence of males feeds back positively on estrus behavior in females. The number of males in the local area, or intruder

pressure, may also explain some variation in male numbers. These data, which are the most extensive for any guenon population, are generally supported by other investigations of different populations and species. The number of sexually active females, as well as intruder pressure, are two important components of female defendability that influence the number of males present in the breeding season in at least three guenon species.

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