Dynamics of male residence and female oestrus during a breeding season of blue monkeys in the Kakamega Forest, Kenya

S. M. Mugatha[1]*, J. O. Ogutu[1], M. Cords[2] and J. M. Maitima[1]

[1]*International Livestock Research Institute (ILRI), PO Box 30709, 00100 Nairobi, Kenya and* [2]*Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, U.S.A.*

Abstract

Blue monkeys (*Cercopithecus mitis stuhlmanni*) are seasonal breeders with a dynamic mating system in which typical one-male social units are regularly disrupted and replaced by multi-male ones. The number of males in the group is correlated with the number of oestrous females. We used observations of male presence and female oestrus on individual days during a 6-month period to assess whether the presence of multiple males in a group stimulates female oestrus or whether oestrous females attract multiple males to the group. We confirmed prior observations with our finding that the number of males in a group was significantly correlated ($r_s = 0.435$, $P < 0.0001$) with the number of oestrous females across 126 observation days. A transition matrix did not show an obvious relationship between day-to-day changes in the numbers of oestrous females and males. However, cross-correlation analysis provided stronger support for the idea that the number of oestrous females attracts males to a group than for the idea that the influx of strange males stimulates oestrus in female blue monkeys. Autocorrelation analysis showed that while female oestrus appeared to show a high degree of synchrony, as expected in a seasonal breeder, there was no evidence that the number of males accompanying a group of females influenced the likelihood of other males joining or leaving the group. Overall, our results confirm that female oestrous behaviour stimulates changes in male residence patterns. However, other observations suggest that changes in male residence may also stimulate female oestrus in some circumstances.

Key words: guenons, male influx, mating system, oestrous

Résumé

Les singes bleus (*Cercopithecus mitis stuhlmanni*) se reproduisent de façon saisonnière selon un système d'accouplement dynamique où des unités sociales typiques, avec un mâle unique, sont régulièrement perturbées et remplacées par des unités avec plusieurs mâles. Le nombre de mâles d'un groupe est lié au nombre de femelles en chaleur. Nous avons enregistré des observations de présence de mâles et de femelles en œstrus jour par jour pendant une période de six mois pour voir si c'est la présence de plusieurs mâles dans un groupe qui stimule les chaleurs chez les femelles ou si ce sont les femelles en chaleur qui attirent les mâles vers le groupe. Nous avons confirmé des observations antérieures en trouvant que le nombre de mâles d'un groupe était strictement lié ($r_s = 0{,}435$, $P < 0{,}0001$) au nombre de femelles en chaleur, pour 126 jours d'observations. Une matrice de transition ne présentait pas de relation évidente entre les changements au jour le jour du nombre de femelles en chaleur et de mâles. Cependant, une analyse de corrélation croisée appuyait plus fortement l'idée que c'est le nombre de femelles en chaleur qui attire les mâles vers un groupe que celle que l'arrivée de mâles étrangers stimule l'oestrus chez les femelles de ces cercopithèques à diadème. Une analyse de l'autocorrélation a montré que, alors que l'œstrus des femelles semble montrer un haut degré de synchronisation - ce que l'on attend de reproducteurs saisonniers - il n'y avait aucune preuve du fait que le nombre de mâles accompagnant un groupe de femelles influence la probabilité que d'autres mâles rejoignent ou quittent le groupe. En général, nos résultats confirment que le comportement des femelles en chaleur stimule les changements du schéma de résidence des mâles. Pourtant, d'autres observations suggèrent que ces changements aussi pourraient, dans certaines circonstances, stimuler l'œstrus des femelles.

**Correspondence:* E-mail: s.mugatha@cgiar.org

Introduction

Reorganization of social units during breeding seasons is not uncommon among animals, including mammals and birds. Such behavioural reorganization may reflect physiological changes that result from seasonal environmental cues, such as photoperiod or temperature shifts (e.g. Pereira, Duarte & Negra, 2004). Here, we explore another mechanism bringing about social reorganization during the breeding season, namely, how behavioural change affects other aspects of behaviour. In particular, we focus on the relationship between the presence of oestrus in females and the variable residence of males in groups of monkeys.

In some primate species, the presence of males in heterosexual groups varies with the season (Borries, 2000; Cords, 2000; Abernethy, White & Wickings, 2002). Blue monkeys, like other African guenons (tribe Cercopithecini), are known for having such a flexible social system (Cords, 1988, 2000). Although the modal social unit is a group of related females, their offspring and a single non-natal adult male, the 3- to 5-month breeding season may include the temporary residence of additional adult males in a group. These males may show continuous or intermittent residence for different periods. Many of them mate with group females. Cords (2002) has distinguished influx from non-influx breeding seasons based on completely nonoverlapping distributions of the percentage of days with multiple males present, the average and maximum numbers of males per day and the duration of visits by males who are not long-term residents. With their highly variable numbers of males present in the group on a given day, influx years provide an opportunity to study the dynamics of male numbers and female reproductive behaviour.

The number of females exhibiting oestrus and the number of males in a group are correlated across years and among days within the breeding season (Cords, 2000, 2002). However, available evidence has not permitted a strong conclusion about whether female oestrus brings males into the group, or whether the presence of males in the group stimulates female oestrus. Cords (2002) examined the chronology of seven breeding seasons, and found that female oestrus preceded the arrival of multiple males in six cases, while the arrival of multiple males preceded the first female oestrus in one. While these results suggest that males may be drawn to groups with multiple oestrous females, the numbers are small, and at least 1 year does not fit the predominant pattern. Furthermore, in this same population, the arrival of a new male in a group whose resident died led to elevated oestradiol levels and sexual activity in females during the nonbreeding season (Pazol, 2003).

Laboratory experiments linking social behaviour and hormone levels provide evidence for causal relationships between female oestrus and male presence that work in both directions. Vandenbergh & Drickamer (1974) and Ruiz de Elvira, Herndon & Wilson (1982) administered hormonal implants to stimulate oestrus in ovariectomized female rhesus macaques outside the normal breeding season. The hormonally primed females stimulated male reproductive activity and gonadal activation. Vandenbergh (1977) documented similar effects in golden hamsters. These results support the idea that female oestrus may stimulate males to attend to females sexually, although the conditions of captivity did not permit males to choose to live with females based on their oestrous status. Other studies have shown that the presence of males, particularly unfamiliar males, may stimulate female oestrus. Mendoza & Mason (1991) found that when a male was introduced into a small group of female squirrel monkeys, the male monkey stimulated their 'breeding readiness', measured in terms of gonadal hormone production and regular cycling. Field observations of our study species have shown that female oestrus may increase precipitously if a new male joins the group (Pazol, 2003). Such observations support zookeeper's lore that reproductively inactive animals can be stimulated to breed by introducing them to unfamiliar mates.

This study aimed to establish whether the influx of extra males into a group of blue monkeys influences the number of females in oestrus or whether it is the oestrous females that attract extra males into the group, based on daily observations of blue monkeys inhabiting the Kakamega Forest, Kenya during a single influx breeding season. If the number of females in oestrus attracts males into the group, then we would expect the number of males in the group to be significantly cross-correlated with the lagged number of cycling females. We would expect the converse to be true if it is the presence of extra-group males that stimulates oestrus in females.

Materials and methods

Study area

The study was conducted at the Isecheno study site of the Kakamega Forest in western Kenya (0°10′–0°21′N, 34°47′–

34°58′E; Cords, 1987). The forest occupies about 12,000 ha of near natural and secondary forest (Lung, 2004) at an altitude of 1500–1700 m. Annual rainfall exceeds 2000 mm, with the major peak from March to August, and a minor peak from September to November. During the study period, rainfall was typical of multi-year norms.

Subjects

The blue monkey (*Cercopithecus mitis stuhlmanni*) population at Isecheno has been under study since 1979. The social group that was the subject of this study, G group, was first observed in 1993 by Mugatha. When the observations reported here were made (24 August 1998–14 February 1999), not all group members could be recognized individually. However, all adult females and adult males were individually known based on natural characters. The group (n = 49) included 17 adult females at that time. Five of these adult females, and one nulliparous large juvenile female, were oestrous during the study period. Eleven adult males were seen within G's home range, six of whom spent time in the group. One of them (HK) was resident in the group throughout the study period.

Data collection

SM followed members of the focal group on 126 days of the 175-day study period, which included the second half of the breeding season (August–September), as well as subsequent months when matings and male visits were rarer, but nevertheless occasionally occurred. Observations were made from 07.00 to 18.30 hours with a 2-h break during midday, when the monkeys were most likely to be resting. When it rained heavily in the afternoons, observations were terminated earlier.

On each observation day, SM kept running notes on which males were present in the group, and recorded all observed social and sexual interactions between adult males and females. Focusing on the males was a good strategy for recording such interactions, as males were easier to follow. Sometimes, it was possible to monitor two males simultaneously, as they courted oestrous females who mostly ranged together. Nevertheless, we also attempted to move around the group to observe as many of its members as possible on a daily basis.

Any female who was seen mating on a given day was followed for several hours in each of the subsequent 2–3 days to record any signs of continued oestrus, such as copulation, semen on genitalia, sexual solicitation of males, or receptivity to courting males. A female was considered to be in oestrus if the female was actually seen mating, had semen on her genitalia and/or actively solicited males by presenting or puckering (Tsingalia & Rowell, 1984).

A male was considered to be 'in' the focal group if the male actually interacted with any member of the group or if the male was <20 m from the group's periphery, a distance at which males are usually attentive to the group (Cords *et al.*, 1986). Males resident in an adjacent group were considered to be part of the study group if they satisfied these conditions. This situation occurred mostly during inter-group territorial encounters. Males are known to copulate with the females of the neighbouring group during such encounters (Cords, 2002).

Data analysis

We used temporal auto- and cross-correlations to analyse the relationships between the numbers of adult males and oestrous females in the group. We were able to accurately record these numbers during 126 observation days; however, samples for our correlation analyses were smaller than this because the observation days were to some degree intermittent. We defined a single period of oestrus as the length of time (measured in days) that a female was observed to show oestrous behaviour, including breaks in observation of 3 days or less. In some cases, gaps in observations prevented us from establishing precisely the onset or termination date of an oestrous period. These cases were excluded from the transition matrix analysis.

Table 1 Frequencies of the number of males and oestrous females sighted daily (n = 126 days) in the study group between August 1998 and February 1999 (e.g. on 34 of 126 days, the focal group had one male and no female in oestrus)

Number of males	Number of females					Total	Mean number of females
	0	1	2	3	4		
0	3	0	0	0	0	3	0.0
1	34	31	10	1	0	76	0.7
2	8	11	8	8	3	38	1.7
3	0	4	3	2	0	9	1.8
Total	45	46	21	11	3	126	
Mean number of males	1.1	1.4	1.7	2.1	2.0		

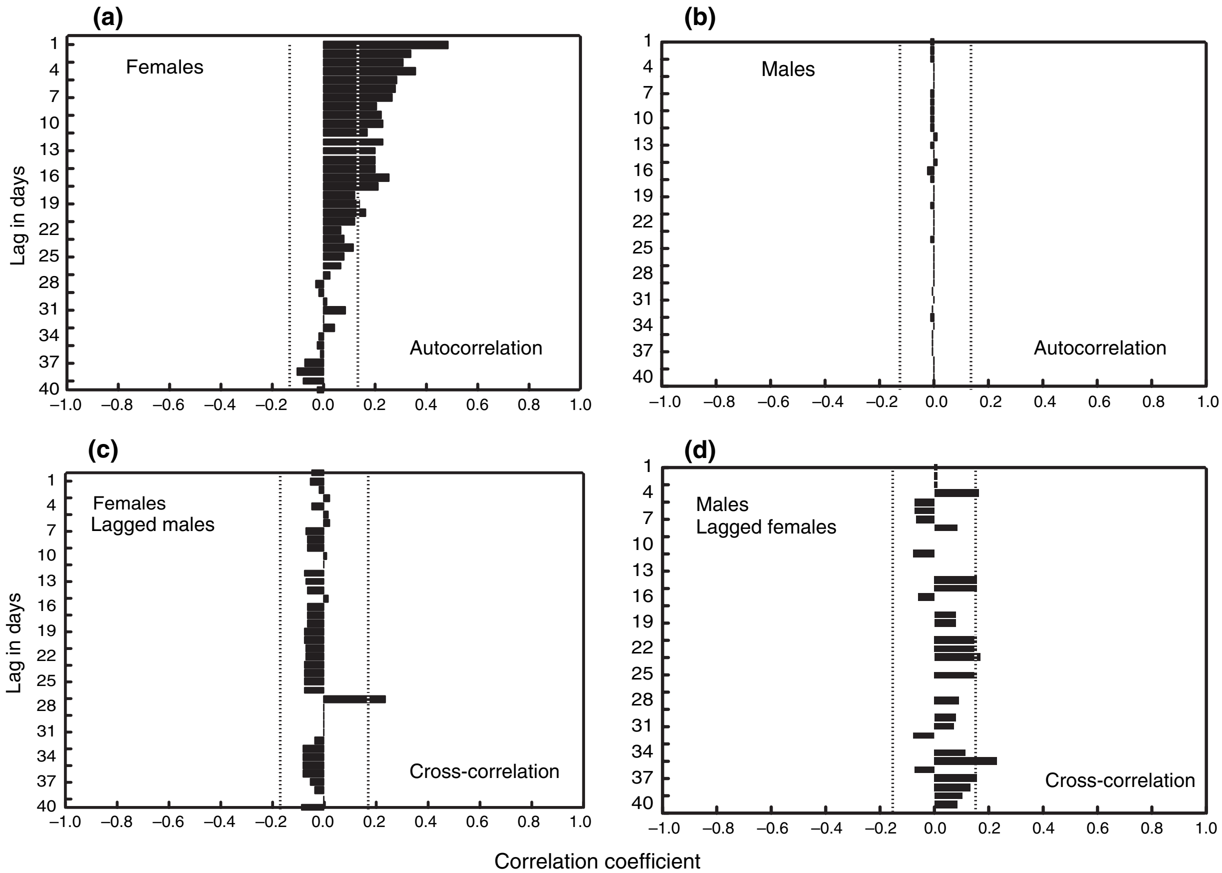

Fig 1 Autocorrelations (a, b) and cross-correlations (c, d) between the numbers of oestrous females and males in the study group. Significant correlation values are indicated by vertical lines

Results

The number of females in oestrus in the focal group

Over the entire study period, the mean number of oestrous females per day was 1.1 ± 1.05 (range 0–4, n = 126 days; Table 1). The six females averaged 13 ± 7.4 days (range 2–22 days) of oestrus over the study period. Two of the six females experienced one continuous period of oestrus, three experienced two short and disjointed periods of oestrus, while one experienced apparently erratic periods of oestrus of variable length. Four of the six receptive females mated with at least two different males; one was seen to mate only with an extra-group male, while the other mated exclusively with the long-term resident male (HK) on days when no other male was present.

Temporal autocorrelation in the number of oestrous females suggests significant positive correlations over the first 4 weeks, followed by a switch to negative correlations thereafter (Fig. 1a). This pattern is consistent with the presence of synchrony in female oestrus, as expected in a seasonal breeder.

The number of males present in the focal group

The number of males sighted in the study group averaged 1.4 ± 0.66 day^{-1}, with 60% of days including only a single male (Table 1). The period of residence in the focal group varied among males. For example, HK was resident in the focal group on all observation days. In contrast, GO resided in the focal group for about 51% of all observation days. Another male, PA, had three short stays dispersed over 8 days, each lasting about 1 day, and constituting only 2% of all observation days.

Temporal autocorrelations in the number of males in the focal group were not significant and showed no discernible

Table 2 Transition matrix showing (a) how often changes in the number of oestrous females from day $t-1$ to t were followed by changes in the number of males from day t to $t+1$ and (b) how often changes in the number of males from day $t-1$ to t were followed by changes in the number of oestrous females from day t to $t+1$ [e.g. there were four occasions in which a decrease in the number of males from day $t-1$ to t was followed by a decrease in the number of oestrous females from day t to $t+1$ (b)]

(a)

Changes in the number of oestrous females from day $t-1$ to t	Changes in the number of males from day t to $t+1$		
	Increase	Decrease	Unchanged
Increase	1	3	3
Decrease	3	2	4
Unchanged	1	2	6

(b)

Changes in the number of males from day $t-1$ to t	Changes in the number of oestrous females from day t to $t+1$		
	Increase	Decrease	Unchanged
Increase	2	2	2
Decrease	2	4	3
Unchanged	5	3	3

pattern (Fig. 1b). The autocorrelogram for males suggests that their visits to the group were temporally independent events, as the number of males present in the focal group on a given day was not related to the number of males present in the group either before or after that day. Thus, it seems that the number of males accompanying a group of females did not significantly influence the likelihood of other males joining or leaving the group.

The relationship between the number of oestrous females and males in the group

Overall, it appeared that days when there were multiple males in the group corresponded with greater numbers of oestrous females (Table 1). In contrast, on days when no male or only one male was present, there were fewer receptive females. The average number of females in oestrus increased monotonically with the number of males, and the average number of males also increased with the number of females in oestrus. The number of males per day was significantly positively correlated to the number of oestrous females per day ($r_s = 0.435$, $P < 0.0001$, n = 126 days), indicating that on days when the number of oestrous females in the group was high, the number of males in the group was also high.

To establish whether it was the number of females in oestrus that attracted males to the group, we examined whether an increase (decrease) in the number of cycling females from day $t-1$ to t was followed by a corresponding increase (decrease) in the number of adult males in the group from day t to $t+1$. Conversely, we examined if an increase (decrease) in the number of males in the group from day $t-1$ to t was associated with a change in the number of cycling females from day t to $t+1$ (Table 2). In general, changes in the number of males in the group were not matched by subsequent changes in the number of oestrous females and vice versa. The cross-correlations were largely statistically insignificant, but the patterns shown by the correlograms (Fig. 1c versus d) seem to provide more support for the idea that the number of females in oestrus attracts males to the group than the idea that the number of males present in a group stimulates female oestrus.

Discussion

Our results show that the number of males present in a group of blue monkeys on a given day is positively associated with the number of oestrous females. These results confirm previous reports by Cords (2002), and support the observation of Cords *et al.* (1986) that typically only one female at a time was seen to be oestrus when there was no multi-male influx during the breeding season. Unlike previous analyses which compared the breeding seasons across several different years or compiled data across multiple years, our analysis focused on one breeding season in detail, thus providing complementary information. One implication of this association between the numbers of males and oestrous females in the group is that females are oestrous synchronously when several males are present in the group. Such synchrony is basic to a mating system in which females mate with multiple partners.

Our analysis provides further evidence that the effect of oestrous females attracting males to a group is stronger than the effect of male presence stimulating oestrus in female blue monkeys. We recommend confirmation of these provisional results with a larger sample. We also note that they concur with Cords' (2002) analysis based on the chronology of events at the beginning of multiple breeding seasons, which revealed that female oestrus normally preceded the arrival of additional males in the group.

How males detect the presence of oestrous females remains an open question. Oestrous female blue monkeys engage in particular behavioural displays, including presenting the hindquarters, puckering the mouth, headflagging and persistent following of males (Tsingalia & Rowell, 1984; Pazol, Carlson & Ziegler, 2002), which are likely visible to males lurking on the edges of groups. Olfactory cues are suggested by observations of males sniffing the genitalia of females before mounting, but we have no information to judge the distance over which relevant information might be transmitted. Our results argue against the idea that males are attracted to groups because other males are already there.

Although our study provides stronger support for the idea that oestrus attracts males, we do not dismiss the possibility that the male presence stimulates oestrus under some circumstances (Pazol, 2003). The behaviour of individual females suggests that they are sexually attracted to unfamiliar males. One of the six oestrous females in our study actively avoided the familiar resident male (HK) to court new ones. Four of the five remaining oestrous females mated with at least one new male, while the remaining female mated only with the familiar resident male (HK) during periods when visiting males were no longer present. Also, when visiting males had gradually left the group in the month of February, there was a rapid decline in the daily number of oestrous females from an average of 1.02 ± 0.6 to 0.3 ± 0.5 ($n = 10$ days after the last male departed). Of course, it is also possible that this decline related to the fact that females had become pregnant.

Acknowledgements

We would like to thank the Ministry of Education, Science and Technology and the Kenya Forest Department for permission to conduct this study. We gratefully acknowledge funding from the U.S. National Science Foundation BCS 98–08273. We would also like to thank the University of Nairobi and the International Livestock Research Institute for facilitating the preparation of the original report and of the manuscript.

References

Abernethy, K., White, L.J.T. & Wickings, E.J. (2002) Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *J. Zool. (Lond.)* **258,** 131–137.

Borries, C. (2000) Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In: *Primate Males* (Ed. P. M. Kappeler). Cambridge University Press, Cambridge, pp. 146–158.

Cords, M. (1987) *Mixed Species Association of Cercopithecus* Monkeys in the Kakamega Forest, Kenya. University of California Press, Berkeley, CA.

Cords, M. (1988) Mating systems of forest guenons. In: *A Primate Radiation: The Evolutionary Biology of the African Guenons* (Eds A. Gautier-Hion, F. Bourliore, J. P. Gautier and J. Kingdon). Cambridge University Press, Cambridge, pp. 323–339.

Cords, M. (2000) The number of males in guenon groups. In: *Primate Males* (Ed. P. M. Kappeler). Cambridge University Press, Cambridge, pp. 84–96.

Cords, M. (2002) When are there influxes in blue monkey groups? In: *The Guenons: Diversity and Adaptation in African Monkeys* (Eds M. E. Glenn and M. Cords). Kluwer Academic/Plenum Publishers, New York.

Cords, M., MItchell, B.M., Tsingalia, H.M. & Rowell, T.E. (1986) Promiscuous mating among blue monkeys of the Kakamega Forest, Kenya. *Z. Tierpsychol.* **72,** 214–226.

Lung, T. (2004) Landbedeckungaenderungen im Gebiet ''Kakamega Forest und assoziierte Waldgebiete'' (Westkenia). *Karlsruher Geowiss. Schr. A* **15,** 1–114.

Mendoza, S.P. & Mason, W.A. (1991) Breeding readiness in squirrel monkeys: female-primed females are triggered by males. *Physiol. Behav.* **49,** 471–479.

Pazol, K. (2003) Mating in the Kakamega Forest blue monkeys (*Cercopithecus mitis*): does female sexual behavior function to manipulate paternity assessment? *Behaviour* **140,** 473–499.

Pazol, K., Carlson, A. & Ziegler, T.E. (2002) Female reproductive endocrinology in wild blue monkeys: a preliminary assessment and discussion of potential adaptive function. In: *The Guenons: Diversity and Adaptation in African Monkeys* (Eds M. E. Glenn and M. Cords). Kluwer Academic/Plenum Publishers, New York, pp. 217–232.

Pereira, R., Duarte, J. & Negra, J. (2004) Seasonal changes in fecal testosterone concentrations and their relationship to the reproductive behavior, antler cycle and grouping patterns in free-ranging male Pampas deer (*Ozotoceros bezoarticus bezoarticus*). *Theriogenology* **63,** 2113–2125.

Ruiz de Elvira, M.C., Herndon, J.G. & Wilson, M.E. (1982) Influence of estrogen-treated females on sexual behavior and male testosterone levels of a social group of rhesus monkeys during the nonbreeding season. *Biol. Reprod.* **26,** 825–834.

Tsingalia, H.M. & Rowell, T.E. (1984) The behavior of adult male blue monkeys. *Z. Tierpsychol.* **64,** 253–268.

Vandenbergh, J.G. (1977) Reproductive coordination in the golden hamster. *Horm. Behav.* **9,** 264–275.

Vandenbergh, J.G. & Drickamer, L.C. (1974) Reproductive coordination among free-ranging rhesus monkeys. *Physiol. Behav.* **13,** 373–376.

(*Manuscript accepted 3 June 2006*)

doi: 10.1111/j.1365-2028.2006.00674.x