*International Journal of Primatology, Vol. 22, No. 2, 2001*

# Correlates of Intergroup Transfer in Male Grey-cheeked Mangabeys

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*Received January 7, 2000; accepted February 17, 2000*

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*We studied factors influencing intergroup transfer in male mangabeys (*Lophocebus albigena*) inhabiting 7 social groups in Kibale National Park over a 2-year period. The sample consisted of 40 males including 36 that we captured and marked during the study. Intergroup transfers are movements between groups that culminate in either long-term (dispersal) or short-term (visits) residency by males in the new groups. Both dispersers and visitors had a greater tendency to move into groups that contained higher numbers of estrous females than their prior group. Using averages of weekly group counts, we found a significant positive relationship between the number of estrous females in a group and the number of adult males in a group, but not between the number of nonestrous females and the number of adult males in the 7 study groups. There is no evidence that dispersal events were released by aggression. For a sample of males followed ≥2 mo before emigration, aggression did not increase just before emigration. Results suggest that spatiotemporal availability of estrous females is a major proximate factor influencing intergroup transfer in mangabeys. The results also suggest that dispersing males are more sensitive to relative numbers of estrous females than to measures of female availability such as operational sex ratio, socionomic ratio, and the number of excess females that take into account the potential for male-male competition.*

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**KEY WORDS:** Mangabeys; Kibale forest; intergroup transfer; primate dispersal.

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## INTRODUCTION

As recently as the mid-1960s, primate social groups were thought to be closed, highly inbred units (DeVore, 1963; DeVore and Washburn, 1963; Nishida, 1966; Lindburg, 1969). Numerous reports from subsequent studies now show that intergroup transfer is a ubiquitous phenomenon in primates (Slatkin and Hausfater, 1976; Henzi and Lucas, 1980; Jones, 1983; Pusey and Packer, 1987). While there is unanimity among researchers about the occurrence of dispersal, suggested proximate causes vary among species and study sites (Smith, 1992). Current evidence suggests that timing and direction of transfer are influenced by 5 main factors: age, number and relatedness of potential sexual partners, number of potential competitors, dominance rank, and agonistic interactions.

In most primate species, young males leave their natal groups before attaining full maturity, perhaps because of attraction to unfamiliar mates (Pusey and Packer, 1987) or to avoid intrasexual competition for mates (Shields, 1987). In certain cases, males may leave groups following aggression from other males (langurs: Boggess, 1979; howlers: Clarke, 1982). For males that have already dispersed once, subsequent dispersals may be related to the availability of receptive females (Pusey and Packer 1987; Sprague, 1992; Smith, 1992) or to changes in rank as in Japanese macaques (Sprague, 1992) and in baboons (Sapolsky, 1996). While male Japanese macaques may join groups where their ranks are likely to be improved or maintained, old male baboons may sometimes disperse following decline in rank. Dispersers respond to other factors as well. Boelkins and Wilson (1972) suggested that high rates of dispersal among rhesus macaques in the Cayo Santiago colony were influenced by high population density. Differences in both density and predation risk might explain differences in dispersal rates between baboons in Amboseli and those at Gombe (Alberts and Altmann, 1995). Timing and rates of dispersal may also be influenced by environmental factors, e.g., bonnet macaque females dispersed following a cyclone (Ali, 1981), and ring-tailed lemurs dispersed following drought (Sussman, 1992).

For primate species with a matrilineal social structure, males may disperse in response to the distribution of social groups formed by philopatric females (Wrangham, 1980; Shields, 1987). Males are thought to respond to two factors: the number and reproductive state of females (Pusey and Packer, 1987; Smith, 1992; Sprague, 1992) and the number of male competitors in a group (Phillips-Conroy *et al.*, 1992). Nevertheless, there are profound differences within and among species. For seasonally breeding species, such as rhesus macaques (Vandenbergh and Vessey, 1968; Lindburg, 1969), vervets (Henzi and Lucas, 1980), Barbary macaques (Paul and Kuester, 1985), Japanese macaques (Sugiyama, 1976), ring-tailed lemurs (Jones, 1983;

Sussman, 1992) and guenons (Cords, 2000), intertroop transfer is often concentrated during the mating season and many social groups are likely to receive immigrants at about the same period. For some species, short-term mating success by new immigrant males does not necessarily increase (Sprague, 1992); in other species such as vervets, individuals might show preference for groups with more kin (Cheney and Seyfarth, 1983). For species, such as baboons, that have no clear mating season (Packer, 1979; Smith, 1992), males tend to transfer into groups in which the number of estrous females is high relative to the number of males. In other species, there is evidence that individuals may also respond to the sex ratio, though this might be site-specific. For example, at Berenty, Madagascar transfer of ring-tailed lemur males appears to be determined by between-group differences in the number of males (Jones, 1983), while at Beza Mahafaly, male-to-female ratio was a better predictor of dispersal direction (Sussman, 1992). Additionally, rhesus male macaques at La Parguera colony, Puerto Rico, left groups with more females in favor of those with fewer females (Drickamer and Vessey, 1973). However, rhesus macaques at the Cayo Santiago colony (Boelkins and Wilson, 1972), vervets (Henzi and Lucas, 1980; Cheney, 1983), and long-tailed macaques (van Noordwijk and van Schaik, 1985) apparently do not respond to sex ratio.

We explore proximate factors implicated in the transfer of mangabey males (*Lophocebus albigena*) between social groups in the Kanyawara study area of Kibale National Park, Uganda. Intergroup movements have not been studied in any detail in *Lophocebus* and *Cercocebus*. We specifically address the following questions: do levels of aggression determine timing of dispersal events? Do mating opportunities influence the decision by males to change social groups? We also compare four different methods of estimating female availability to determine which best predicted dispersal in mangabeys.

## METHODS

### Study Area and Subjects

We worked in the Kanyawara study area of Kibale National Park, Uganda. Kibale National Park (0°13′–0°41′ N and 30°19′–30°32′ E) is a tropical rain forest, situated along the eastern edge of the western rift valley, near the foothills of Mt. Rwenzori (Struhsaker, 1997). The park, elevated along a north-south gradient (1590–1110 m), is a mosaic of logged forest, unlogged forest, grassland, swamp, and plantation. Kibale is renowned for its 11 primate species including the grey-cheeked mangabey, *Lophocebus albigena*.

Kanyawara study area (0°34′ N, 30°22′ E) is located at the northwestern edge of the park. The area receives a bimodal seasonal distribution of rainfall averaging 1670 mm/year, based on data collected between 1977–1994 (Chapman and Chapman, 1997). March–May and September–November are the wettest periods (Struhsaker, 1997). Details of the study area are provided by Wing and Buss (1970), Kingston (1967), and Struhsaker (1975, 1997).

The subjects are male mangabeys. Mangabeys at the study site have been subjects in several other studies (Waser and Floody, 1974; Waser, 1977; Wallis, 1978; Freeland, 1980; Olupot, 1994; Olupot *et al.*, 1994). Kibale mangabeys live in multimale groups averaging 14 individuals (Waser, 1977; Wallis, 1978; this study). Our study focused on males belonging to 7 social groups, which ranged from 5 to 25 individuals and averaged 16.4 (BU group), 14 (LC group), 12.8 (MK group), 9.5 (MKB group), 14.9 (UC group), 21.1 (CC group), and 14.6 (NY group) individuals during the 24-mo study. The groups contained a median number of three adult males (range 1–10), zero or one subadult male, and $\leq 3$ juvenile males.

## Field Methods

We contacted study groups in May 1996 and followed them systematically, beginning in 1997. Individual *Lophocebus albigena* were difficult to distinguish using natural features. To facilitate recognition and focal animal follows, we captured and radiotagged 21 adult males, 3 subadult males, and 3 large juvenile males in the 7 groups (Olupot, in press). We captured an additional 9 males and gave them collars without radios (or radios failed). We attempted to collar all adult males within the study site (approximately 5 × 6 km) but $\geq 4$ unmarked adult males were in the study area for various periods of time. Age-class categories follow Waser (1977). We report results from regular follows of the 7 groups in which males were radiotagged (3 groups, January 1997 to November 1998; 3 groups, May 1997 to November 1998; one group, August 1997 to November 1998).

Routine censuses of social troops have been used to document dispersal in primates (Drickamer and Vessey, 1973; Alberts and Altmann, 1995). To keep records of male immigrations and emigrations, as well as female availability in each social group during the study, we censused individual groups several times a week to obtain accurate counts. During each census, we scored the identity, age, and sex of each individual and the estrous state of each female as the group traversed crossing points in the canopy.

Initially, we followed radiocollared adult males on a focal basis, but rates of interaction of any sort were exceedingly low when males were chosen at random. Adult male interactions were much more frequent in the presence of estrous females. Therefore, we followed mostly estrous females, and occasionally nonestrous females in each study group on a focal basis and scored agonistic and affiliative interactions of all nearby males. We categorized females as estrous or nonestrous by visual examination of the sexual skin, which swells during the follicular phase and shrinks during the luteal phase (Wallis, 1983). Rain, dense foliage and undergrowth, as well as wide scattering of individuals sometimes prevented data collection. Whenever conditions permitted, we recorded the identity of the male nearest to the focal female at predetermined 5-min intervals. We noted aggressions and supplantations among males in the vicinity of the target female, groomings and approach-avoidance interactions between males and the target female, and copulations whenever observed. Three well-trained assistants aided in data collection so that several females from the same group or in different groups could be followed simultaneously.

In all social interactions, we recorded the identities of males involved by the color codes of the collar and/or radio-transmitter. If a male did not have artificial marks, we noted his age class. Depending on the nature of the social interaction, we recorded the status of each male during the interaction as charger, chargee, supplanter, supplantee, groomer, and groomee. Individual A charged B if A lunged at, chased, grabbed, scratched, bit, or wrestled with individual B. Supplantations occurred if individual A approached individual B, which left, and A took the spot of B. Approach was scored if an individual (A) made a directed movement towards another (B). Individual B was regarded as having avoided A if A moved to $\leq 5$ m of B, which then moved to a spot further from A. Because grooming in primate species may occur in a sexual context (Sanchez-Villagra *et al.*, 1998), we recorded instances of grooming on initial occurrence and at 5-min intervals when continued thereafter. We scored sexual presents and copulations following the criteria of Wallis (1983). Our study yielded 1654 hr of focal estrous female, and 134 hr of focal nonestrous female data. We recorded additional field notes *ad libitum* (Altmann, 1974) for all males.

## Definition of Terms

The most frequently used terms in the primate dispersal literature are variously defined by authors. We follow Lindburg (1969) by scoring a transfer on sighting any individual male within the vicinity of a group other than his group of origin (in this study, <50 m from the nearest group member in most cases, and always <200 m). We follow Shields (1987) in defining dispersal as the movement of an individual from its site or group of origin to its first or subsequent breeding site. If the male left the new group without evidence of mating, the transfer is a visit (cf. transient dispersal: Glander, 1992). The possibility that some visiting males might have copulated cannot be ruled out. However, all cases defined as visits resulted in relatively short stays (maximum 14 days), much shorter than the shortest dispersal (minimum 68 days: Olupot, 1999), reinforcing the possibility that dispersals are a distinct class of transfers. When a mangabey dispersed, we defined emigration as leaving the prior group and immigration as entering a new group. If the male spent weeks or months moving independently of and usually >200 m away from any mangabey group, he was solitary.

We witnessed 26 cases of dispersal and 27 visits. However, for a variety of reasons our data from many of these cases are incomplete. Some dispersing males were initially tagged either when they were solitary ($n = 1$), or shortly after appearing as new, unmarked males in the study groups ($n = 15$). Others ($n = 3$) emigrated to unhabituated groups where we could not obtain reliable group counts or focal follows. Still others ($n = 9$) had collars without functioning radios. We restricted analyses of male behaviors surrounding dispersal to radiotagged males for which we had substantial numbers of focal samples through the relevant part of the dispersal process. Similarly, we restricted analyses of male behaviors before visits to cases in which radiocollared males were resident in one group (rather than solitary) and were sighted in a second group but returned to the original group within 1–2 days.

## Hypothesis Testing

To determine if levels of aggression determine timing of dispersal events, we examined the following predictions: 1) Aggression levels towards each dispersing male should increase immediately before emigration. We examined this possibility using 6 dispersals and 7 visits for which aggression data from focal samples were available for ≥8 weeks before the male left his group. 2) Males should transfer into groups in which they receive less aggression than they did before dispersal. Our sample for this comparison is restricted to 5 dispersals for which we had ≥4 weeks of focal samples both before emigration and after immigration. 3) Males should transfer into groups containing fewer males of their age class. We examined this possibility using a sample of 5 dispersals and 9 visits for which we had reliable counts of both groups during the weeks of emigration and immigration or during the week of the visit.

To determine if mating success is a factor determining the decision of males to leave and enter particular groups at a particular time, we tested the following predictions:

1. There should be a positive relationship between the number of males and the number of estrous females in the group. We tested this by

averaging the weekly counts of males and estrous females for each of the 7 study groups over the entire study, and regressing the averages for males on the female averages. As a control, we regressed the numbers of males against the numbers of nonestrous females.

2. For each transfer event, there should be a higher availability of estrous females in the new than in the prior group. We compared female availability in two ways, using the 5 dispersals and 9 visits for which group counts were available both before and after the event. First, we evaluated female availability in the short term. For each dispersing male, we measured female availability in its prior group during the week immediately preceding emigration, and in its new group during the week immediately following immigration. Secondly, we compared average female availability in new and prior groups over the 25 weeks after immigration. This gave us a longer-term measure of the availability of mating opportunities to the dispersed male in its new group, compared to the availability it would have experienced had it not dispersed.

   In both cases, we estimated female availability in the following four ways: a) the ratio of adult females to adult males (socionomic ratio, SR), b) the ratio of the number of estrous females to adult males [operational sex ratio, OSR), c) the number of excess females calculated as the difference between the number of estrous females and the number of males, and d) the absolute number of estrous females. Because the first three of these measures incorporate the numbers of males as well as females, they reflect the potential intensity of mate competition as well as the potential number of offspring that could be fathered.

3. The number of copulations by dispersed males should be higher in the new group than in the prior group. We examined this possibility for the 5 dispersals for which we had focal records $\geq$4 weeks before and after dispersal. Ideally, scores of copulations would suffice to do this. However, copulations are rare, and a large proportion of events that occur may not be observed. Therefore, we also examined the frequencies with which males were involved in behaviors correlated with copulations.

   From data in all focal female samples throughout the study (Table I), we calculated rates of interaction per 12 hr for each male if recognizable by artificial marks, or for each class of male for individuals that were not marked. For each male or class of males, we based calculations only on samples in which the male(s) were in the group during the focal sample. We used these rates in a hierarchical cluster analysis to generate a tree describing associations

**Table I.** Rates of social interactions involving males per 12 hours, recorded during 1788 hours of focal female follows as described in text*

| Label | NN | Fapproach | Mavoid | Mapproach | Favoid | Present | Cop | Grmer | Grmee | Charger | Chargee | Suppter | Supptee |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AM | 18.735 | 2.066 | 0.355 | 1.743 | 0.312 | 2.431 | 0.764 | 0.118 | 1.689 | 0.689 | 0.581 | 0.387 | 0.237 |
| BB | 42.968 | 1.771 | 0.156 | 3.907 | 0.573 | 2.761 | 1.094 | 0.208 | 2.969 | 0.573 | 0.000 | 0.781 | 0.104 |
| BG1 | 41.677 | 3.310 | 0.000 | 2.793 | 0.103 | 3.724 | 1.138 | 0.414 | 3.414 | 1.138 | 0.000 | 0.724 | 0.000 |
| BKC | 52.820 | 5.340 | 0.000 | 5.026 | 0.000 | 5.340 | 0.942 | 0.000 | 3.141 | 0.942 | 0.000 | 0.314 | 0.000 |
| BLUE | 23.588 | 1.413 | 0.257 | 1.285 | 0.308 | 1.028 | 0.257 | 0.257 | 1.002 | 0.771 | 0.257 | 0.257 | 0.308 |
| GR | 15.610 | 0.845 | 0.058 | 0.903 | 0.117 | 0.787 | 0.379 | 0.204 | 0.787 | 1.835 | 0.146 | 0.408 | 0.058 |
| GREEN | 35.211 | 1.500 | 0.197 | 1.263 | 0.237 | 1.105 | 0.197 | 0.276 | 1.223 | 1.302 | 0.039 | 0.553 | 0.118 |
| GYG | 70.090 | 2.926 | 0.300 | 2.026 | 0.150 | 2.401 | 1.275 | 0.300 | 2.476 | 1.200 | 0.075 | 0.825 | 0.000 |
| JUV | 13.453 | 1.251 | 0.152 | 3.129 | 0.168 | 0.722 | 0.104 | 0.890 | 1.492 | 0.176 | 0.545 | 0.152 | 0.610 |
| LG | 20.019 | 1.384 | 0.231 | 0.922 | 0.000 | 0.922 | 0.231 | 0.000 | 0.461 | 0.000 | 0.461 | 0.000 | 0.461 |
| LGYG | 12.882 | 0.545 | 0.073 | 0.800 | 0.000 | 0.509 | 0.073 | 0.073 | 1.018 | 0.182 | 0.145 | 0.145 | 0.291 |
| LM | 19.647 | 1.506 | 0.137 | 1.187 | 0.137 | 1.004 | 0.183 | 0.228 | 1.369 | 0.548 | 0.365 | 0.456 | 0.000 |
| MM | 37.509 | 3.001 | 0.000 | 0.965 | 0.322 | 0.107 | 0.000 | 0.214 | 0.429 | 0.000 | 0.214 | 0.000 | 0.429 |
| MYG | 10.533 | 0.653 | 0.052 | 1.072 | 0.287 | 0.183 | 0.105 | 0.235 | 0.549 | 0.026 | 0.157 | 0.026 | 0.235 |
| OG | 10.195 | 1.270 | 0.127 | 0.889 | 0.095 | 1.397 | 0.286 | 0.190 | 1.365 | 0.190 | 0.063 | 0.317 | 0.095 |
| RB | 14.767 | 3.041 | 0.608 | 0.304 | 0.608 | 0.608 | 0.000 | 0.912 | 0.000 | 0.000 | 0.304 | 0.304 | 0.000 |
| REC | 20.581 | 0.943 | 0.000 | 2.061 | 0.105 | 1.118 | 0.280 | 0.175 | 1.048 | 0.489 | 0.349 | 0.314 | 0.175 |
| RED | 45.376 | 5.278 | 0.259 | 4.502 | 0.155 | 6.986 | 2.070 | 0.052 | 2.743 | 0.931 | 0.673 | 0.724 | 0.207 |
| RM | 17.464 | 1.208 | 0.302 | 0.201 | 0.302 | 0.604 | 0.201 | 0.101 | 0.906 | 0.403 | 1.509 | 0.302 | 0.302 |
| RR | 40.162 | 2.115 | 0.043 | 3.670 | 0.345 | 2.849 | 0.518 | 0.432 | 2.634 | 0.734 | 0.345 | 0.777 | 0.000 |
| SAM | 7.988 | 0.613 | 0.161 | 0.775 | 0.065 | 0.484 | 0.177 | 0.000 | 0.210 | 0.032 | 0.226 | 0.161 | 0.290 |
| WB | 18.127 | 1.309 | 0.091 | 1.583 | 0.152 | 1.126 | 0.426 | 0.000 | 0.822 | 0.487 | 0.122 | 0.213 | 0.030 |
| WM | 18.332 | 1.634 | 0.105 | 0.580 | 0.158 | 2.056 | 0.738 | 0.105 | 1.423 | 0.264 | 0.105 | 0.527 | 0.000 |
| WR | 18.013 | 0.876 | 0.204 | 1.139 | 0.029 | 0.993 | 0.321 | 0.088 | 1.051 | 0.438 | 0.029 | 0.088 | 0.058 |
| YB | 20.665 | 1.531 | 0.000 | 1.531 | 0.328 | 0.547 | 0.219 | 0.000 | 1.968 | 0.328 | 0.328 | 0.328 | 0.219 |
| YBK | 14.590 | 0.478 | 0.028 | 1.433 | 0.112 | 0.702 | 0.337 | 0.140 | 0.253 | 0.056 | 0.253 | 0.084 | 0.169 |
| YM | 56.385 | 3.273 | 0.401 | 3.673 | 0.668 | 3.874 | 1.737 | 0.334 | 3.139 | 1.002 | 0.334 | 0.267 | 0.000 |
| YR | 15.664 | 0.595 | 0.028 | 1.303 | 0.198 | 0.849 | 0.538 | 0.113 | 0.821 | 0.311 | 0.708 | 0.311 | 0.142 |

*Samples from marked males that were usually solitary (located in groups for less than 20 hr of focal female follows) are excluded. The label "AM" represents pooled data from at least 10 newly immigrated, unmarked adult males; SAM represents pooled data from unmarked subadult males; JUV represents pooled data from large juvenile males. Other entries are for individual males: MYG was an old juvenile; YBK, MM, and RB were subadults, the rest of the males were adult. Abbreviations for social interactions: NN = times the male is scored as the focal female's nearest neighbor; Fapproach = Female approaches male, Mavoid = Male avoids female, Mapproach = Male approaches female, Favoid = Female avoids male, Present = Female presents sexually to male, Cop = Copulation, Grmer = Male grooms female, Grmee = Male is groomed by female, Charger = Male charges at other males, Chargee = Male is charged by other males, Suppter = Male supplants other males, Supptee = Male supplanted by other males.

among various social interactions and to determine which of those interactions had rates that were significantly associated with rates of observed copulation.

We entered all data in Microsoft Excel and analyzed them using Dbase and Systat (Wilkinson, 1998).

# RESULTS

## Do Levels of Aggression Determine Timing of Transfers?

Radiocollared males were charged and supplanted at widely varying rates in different months, but aggression was generally rare and changes in rates of aggression were not obviously related to the timing of intergroup transfers. One out of six males received aggression at a higher rate during the month preceding dispersal than during prior months, but three showed the reverse pattern (Table II). Similarly, none of the six males visiting other groups received aggression at higher rates in the month immediately

**Table II.** Rates (per 12 hours) at which males that dispersed or visited other groups were recipients of aggressive encounters (charging and supplantation) during the four weeks immediately before emigration and during all prior focal samples in the same group. Sample sizes (minutes of focal observation) are in parentheses; P values are from Wilcoxon matched-pairs tests. For each dispersal or visit, the higher rate is indicated in boldface

| | Male | 4 weeks immediately before emigration | Prior samples |
|---|---|---|---|
| Dispersals | | | |
| | LM | 0.00 (1038) | **0.74** (7745) |
| | OG | 0.00 (550) | 0.00 (640) |
| | RB | **0.74** (973) | 0.00 (1180) |
| | RM | 0.48 (1502) | **2.16** (5653) |
| | WM1 | 0.00 (175) | 0.00 (785) |
| | WM2 | 0.00 (235) | **0.43** (5030) |
| | Median | 0.00 | **0.37** |
| | P | 0.36 | |
| Visits | | | |
| | GREEN | 0.00 (1724) | 0.00 (2343) |
| | GYG | 0.00 (1730) | 0.00 (1947) |
| | LGYG | 0.00 (1265) | **0.58** (1240) |
| | LM | 0.00 (775) | **1.93** (2990) |
| | RED | 0.00 (2612) | **1.33** (9185) |
| | WM | 0.00 (175) | 0.00 (785) |
| | YB | 0.00 (755) | 0.00 (475) |
| | Median | 0.00 | 0.00 |
| | P | 0.11 | |

**Table III.** Rates (per 12 hours) at which males that dispersed were recipients of aggressive encounters (charging and supplantation) in the month immediately preceding emigration and the month immediately following immigration. Sample sizes (minutes of focal observation) are given in parentheses; P value is from a Wilcoxon matched-pairs test. For each dispersal, the higher rate is indicated in boldface

| | Aggression received | |
|---|---|---|
| Male | 4 weeks before emigration | 4 weeks after immigration |
| LM | 0.00 (1038) | **0.20** (3664) |
| OG | 0.00 (550) | 0.00 (1295) |
| WM1 | 0.00 (175) | 0.00 (1016) |
| WM2 | 0.00 (235) | 0.00 (4389) |
| YB | 0.00 (755) | **2.13** (1016) |
| Median | 0.00 | 0.00 |
| P | 0.18 | |

preceding the visit than he had earlier, and three showed the reverse pattern.

There is no evidence that rates at which males received aggression were reduced following dispersal (Table III). Two of five males were charged or supplanted at higher rates during the month following dispersal than during the previous month.

There is no evidence that males dispersed into groups with fewer males to escape aggression. In four out of five cases of dispersal, males moved into groups containing more adult males than were in their prior group. Similarly, six out of nine visits were to groups with more adult males.

### Do Mating Opportunities Influence the Decision by Males to Change Social Groups?

Overall, there is a positive relationship between the number of adult males and the number of estrous females in a group (Least squares regression: $r_5^2 = 0.68$, $p = 0.02$; Fig. 1). However, there is no relationship between the number of adult males and the number of nonestrous females in groups (least-squares regression: $r_5^2 = 0.06$, $p = 0.58$). Correlational data do not, of course, indicate causation. A stronger test of the importance of estrous females in provoking immigration can be obtained by comparing estimates of female availability in prior and new groups during the week of transfer and over several weeks after, for each instance of transfer.

Four out of five dispersing males immigrated into groups with more estrous females during the week of immigration than had been present in their prior group (Table IVa). In all five cases, the male dispersed to a group that had as many or more estrous females than his original group. All five

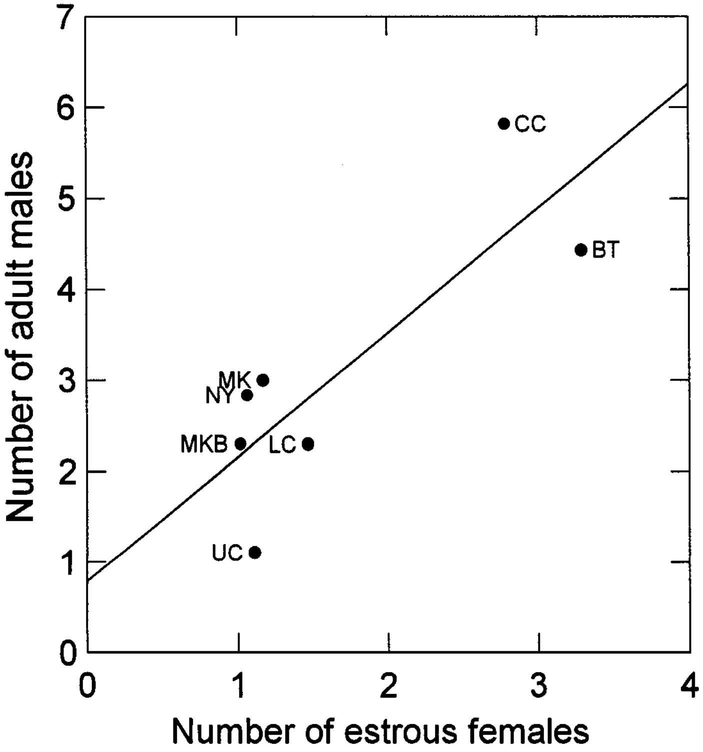

**Fig. 1.** Relationship between the number of adult males and estrous females in a group. Plotted values are overall means based on weekly group counts (n = 100 weeks for BT group, 77 weeks for CC group, 99 weeks for LC group, 96 weeks for MK group, 67 weeks for MKB group, 83 weeks for NY group, and 84 weeks for UC group).

males immigrated into groups containing more estrous females, on average, than their prior group during the 25 subsequent weeks (Table IVa). In both the short and the long term, the median number of females in a dispersing male's new group was three times the median in the prior group.

Similarly, in 6 out of 9 cases males visited groups containing more estrous females than their own, and 8 out of 9 visits were to groups that had more estrous females, on average, over the next 25 weeks (Table IVb).

Number of estrous females was a more reliable predictor of the group into which males immigrated than operational sex ratio was. Socionomic ratio and the number of excess females were the least predictive measures of groups into which males transferred (Table IVa,b).

Several types of behavior recorded during focal samples are highly correlated with rates of copulation (Fig. 2). Males with higher than average rates

**Table IV.** Short- and long-term comparisons of female availability in prior and new groups during cases of intergroup transfer [number of Estrous Females (EF), Socionomic Ratios (SR), Operational Sex Ratios (OSR), and Excess Females (EXF)]. Table IVa: dispersal, Table IVb: visits. P values are from Wilcoxon matched-pairs tests; for each comparison, the higher index is in boldface

| | EF | | OSR | | SR | | EXF | |
|---|---|---|---|---|---|---|---|---|
| Male | Prior | New | Prior | New | Prior | New | Prior | New |
| | | | | Table IVa | | | | |
| Week of dispersal | | | | | | | | |
| LGYG | 2.00 | 2.00 | **0.67** | 0.50 | **2.67** | 2.00 | **−1.00** | −2.00 |
| LM | 1.00 | **3.00** | 0.50 | **0.60** | **3.00** | 1.60 | **−1.00** | −2.00 |
| OG | 0.00 | **5.00** | 0.00 | **1.12** | 1.33 | **2.00** | −3.00 | **1.00** |
| WM1 | 1.00 | 1.00 | 0.14 | **0.33** | 1.14 | **1.67** | −6.00 | **−2.00** |
| WM2 | 1.00 | **4.00** | 0.25 | **0.67** | 1.50 | 1.50 | −3.00 | **−2.00** |
| Median | 1.00 | **3.04** | 0.34 | **0.53** | **2.82** | 1.61 | **−1.56** | −2.68 |
| P | 0.11 | | 0.14 | | 0.47 | | 0.34 | |
| Subsequent 25 weeks | | | | | | | | |
| LGYG | 1.00 | **3.04** | 0.39 | **0.57** | **2.82** | 1.61 | **−1.56** | −2.54 |
| LM | 1.00 | **3.96** | **0.96** | 0.60 | **5.00** | 1.20 | **−0.08** | −2.76 |
| OG | 0.42 | **2.96** | 0.34 | **0.53** | **2.11** | 1.59 | **−1.27** | −2.68 |
| WM1 | 0.60 | **3.36** | 0.28 | **0.49** | **2.84** | 1.30 | **−1.76** | −3.64 |
| WM2 | 1.12 | **1.40** | 0.23 | **0.46** | 1.42 | **1.77** | −2.80 | **−1.72** |
| Median | 1.00 | **3.04** | 0.34 | **0.53** | **2.82** | 1.61 | **−1.56** | −2.68 |
| P | 0.04* | | 0.50 | | 0.08 | | 0.34 | |
| | | | | Table IVb | | | | |
| Week of visit | | | | | | | | |
| GREEN | 1.00 | **2.00** | **1.00** | 0.33 | **6.00** | 2.33 | **0.00** | −1.00 |
| GYG | 1.00 | **5.00** | **1.00** | 0.75 | **7.00** | 2.00 | **0.00** | −1.00 |
| LGYG1 | 2.00 | 2.00 | 0.67 | **1.00** | **3.50** | 2.67 | 0.00 | **2.00** |
| LGYG2 | 1.00 | 1.00 | 0.25 | **0.50** | 2.25 | **3.00** | −3.00 | **−1.00** |
| LM1 | 1.00 | **3.00** | 0.33 | **1.00** | **1.67** | 1.00 | −2.00 | **0.00** |
| LM2 | 1.00 | **2.00** | 0.33 | **0.67** | **1.67** | 1.00 | −2.00 | **−1.00** |
| LM3 | 0.00 | **2.00** | 0.00 | **0.67** | 1.67 | **2.67** | −3.00 | **−1.00** |
| RED | 2.00 | 2.00 | **0.67** | 0.25 | **2.67** | 1.00 | **−1.00** | −6.00 |
| WM | 1.00 | **3.00** | 0.33 | **1.50** | 1.67 | **3.00** | −2.00 | **1.00** |
| Median | 1.00 | **2.00** | 0.33 | **0.67** | **2.67** | 2.33 | −2.00 | **−1.00** |
| P | 0.03* | | 0.26 | | 0.31 | | 0.25 | |
| Subsequent 25 weeks | | | | | | | | |
| GREEN | 1.60 | **3.32** | 0.61 | **0.79** | **2.67** | 1.57 | −1.08 | **−0.92** |
| GYG | 0.84 | **3.24** | **0.82** | 0.61 | **6.46** | 1.56 | **−0.24** | −2.08 |
| LGYG1 | 1.00 | **3.04** | 0.39 | **0.60** | **2.43** | 1.13 | **−1.56** | −2.12 |
| LGYG2 | **3.12** | 1.00 | **0.55** | 0.50 | 1.49 | **3.17** | −2.72 | **−1.08** |
| LM1 | 0.54 | **0.64** | 0.17 | **0.31** | **1.93** | 1.35 | −2.46 | **−1.56** |
| LM2 | 0.92 | **2.64** | 0.27 | **1.66** | 1.69 | **3.83** | −2.44 | **−1.96** |
| LM3 | 0.56 | **0.78** | 0.17 | **0.24** | **2.08** | 1.04 | **−2.44** | −2.48 |
| RED | 1.27 | **4.04** | **0.65** | 0.52 | **3.42** | 1.01 | **−0.85** | −3.72 |
| WM | 1.40 | **3.20** | 0.46 | **1.26** | 1.31 | **1.84** | −1.72 | **0.52** |
| Median | 1.00 | **3.04** | 0.46 | **0.60** | **2.08** | 1.56 | **−1.72** | −1.96 |
| P | 0.07 | | 0.14 | | 0.31 | | 0.86 | |

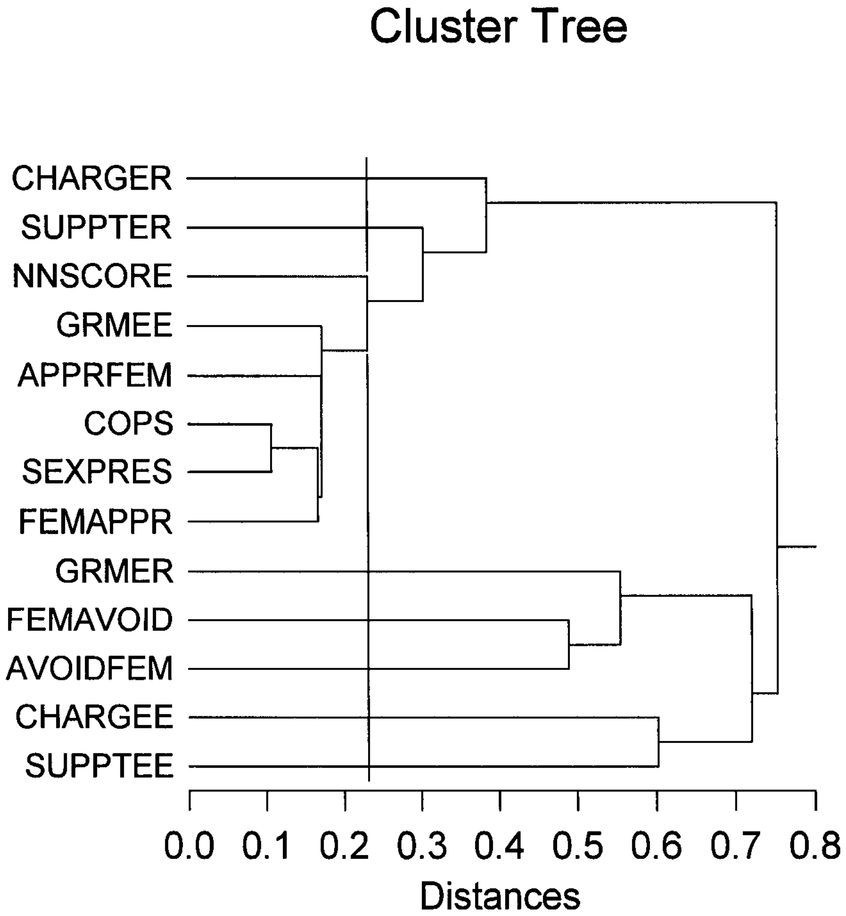

**Fig. 2.** A hierarchical cluster tree depicting the association between male mating success (COPS) and sexual presents by estrous females (SEXPRES), groomings received (GRMEE) or given (GRMER), rate at which males approached females (MAPPR) and were avoided by females (FAVOID), rate of female approach to males (FAPPR) and were avoided by males (MAVOID), frequency of nearest-neighbor scores of males to females (NN), supplantations and fights initiated or received by males (SUPPTER and CHARGER, SUPPTEE and CHARGEE). The tree is constructed from the Pearson correlation matrix of rates per 12 hr in Table I. Clustering is based on Euclidean distances. The vertical line cutting across tree branches represents a 95% cut-off region. Variables with branches to the right of the line are not significantly correlated with one another.

of copulation were more frequently the nearest neighbors of estrous females; estrous females more commonly presented to them sexually and groomed them, and they approached and were approached by estrous females more often. Males often involved in copulations also had high rates of charging and

**Table V.** Rates per 12 hr of mating and behaviors associated with high mating success for five dispersing males during focal samples the 4 weeks preceding emigration and the 4 following immigration. P values are from Wilcoxon matched-pairs tests

| Variable | Median (range) before emigration | Median (range) after immigration | P |
|---|---|---|---|
| Copulations | 0.00 (0.00–1.31) | 0.20 (0.00–0.71) | 0.29 |
| Sexual presents | 0.00 (0.00–1.91) | 0.79 (0.00–2.78) | 0.07 |
| Female approaches male | 0.00 (0.00–4.77) | 1.18 (0.00–5.67) | 0.07 |
| Male approaches female | 0.00 (0.00–3.93) | 1.42 (0.39–2.22) | 0.69 |
| Male is groomed by female | 0.00 (0.00–1.31) | 0.98 (0.00–1.56) | 0.11 |
| Male is female's nearest neighbor | 23.8 (2.62–30.60) | 9.35 (2.88–17.70) | 0.14 |

supplanting other males, but these behaviors were less significantly related to each other.

For the five males followed $\geq$4 weeks before and after dispersal, we detected no significant difference between rates of copulation or any of these related behaviors before and after dispersal. However, median rates of copulation, grooming and sexual presenting by the estrous female, approaching by females to males and vice versa were all higher after immigration than before emigration (Table V).

## DISCUSSION

### Do Levels of Aggression Determine Timing of Intergroup Transfer?

An increase in agonistic encounters immediately preceded transfer in only one out of 13 cases. Five out of five dispersing males received as much or more aggression in their new groups as they had in the ones they left, and ten out of 14 males dispersed or visited groups with more males than their prior group. This suggests that mangabeys did not disperse to avoid aggression. In this respect, mangabeys may be similar to other Old World monkey species, such as baboons (Smith, 1992), rhesus macaques (Boelkins and Wilson, 1972; Drickamer and Vessey, 1973), and Japanese macaques (Sugiyama, 1976). They differ from cercopithecine species such as patas monkeys (Hall, 1965) and vervets (Henzi and Lucas, 1980), in which dispersal is often preceded by aggression. Although mangabeys are known to communicate aggressively through facial expressions (Das *et al.*, 1998) and head gestures (Wallis, 1983), it is unlikely that any threatening facial expressions or gestures caused individuals to leave without actual fights or supplantations.

## Do Mating Opportunities Influence the Decision by Males to Transfer?

In the majority of dispersal and visiting events, there were more estrous females in the new group than in the prior group, both in the short and in the long term. When males dispersed, they dispersed to groups that contained as many or more estrous females than other groups in the vicinity. This suggests that most dispersers and visitors responded to both spatial and temporal availability of estrous females. The response appears to be more clearly linked to the absolute number of estrous females than to indices of female availability that incorporate the number of competing males, including socionomic ratio or operational sex ratio (Cheney and Seyfarth, 1983; Sussman, 1992, Agoramoorthy and Rudran, 1993). Visits and dispersals show similar patterns, suggesting that most visits may have been attempted dispersals. In a few cases, visits appeared to be cases of active resource defense wherein a male attempted to deflect the adjacent group from part of his home range.

Mangabeys appear to conform to the pattern reported in other primate species (chimpanzees: Pusey, 1980; Goodall, 1983; Hiraiwa-Hasegawa, 1984; baboons: Smith, 1992; rhesus macaques: Lindburg, 1969; Japanese macaques: Sprague, 1992; vervets: Henzi and Lucas, 1980; guenons: Cords, 2000) in that attraction to social units with potential mates is an important proximate cause for dispersal. The tendency by males to move to groups with more sexually receptive females may be even stronger than it appears, for at least four reasons. First, we distinguished estrous females simply by the presence of swollen sexual skin. Accordingly, focal samples include not only some nonestrous females, but also some estrous females with pre- or post-peak swellings. Assuming that mangabey cycles resemble those of baboons, these females were likely not fertile and may have been less attractive to mangabey males (Saayman, 1970; Wildt *et al.*, 1977; Wallis, 1983). Secondly, not all males that attempted to immigrate in response to estrous females may have succeeded in doing so. Indeed, although there is no evidence that emigrating residents escaped aggression, several visiting males were driven out of groups by residents shortly after they entered them. Thirdly, males might have incomplete knowledge about the numbers of estrous females in neighboring groups.

Fourthly, we may have underestimated the gain in reproductive opportunities realized by dispersing males: it is possible that some females in prior groups may be related to the dispersing males and avoid mating with them, so that our counts overestimate the number of mating opportunities there. Packer (1979) found that baboons involved in natal dispersal did not necessarily move to groups with more females, while those involved in secondary transfers did. Because most subject males were marked as adults, we suspect that most of the dispersal events we witnessed represent secondary transfers. However, some of them may represent natal dispersal, in which case they presumably gained access to outbred mating opportunities.

For the sample of males considered, we did not detect a significant increase in measures of mating success following dispersal. This might conceivably reflect a tendency for new immigrants to mate inconspicuously, in which case such matings would be underrepresented in our data. However, mangabey females produce distinctive postcopulatory vocalizations (Wallis, 1983) so that matings tend to be both visually and acoustically conspicuous. It is more likely that our failure to detect a significant increase in mating success reflects the small sample of dispersal events under consideration. Although we observed 26 dispersals, pre-emigration data are not available for most males. Postimmigration focal observations from males RED, LGYG, BB, and YB, none of which were the subject of focal samples before emigration, suggest that immigrating males often mate at high rates. These males attained copulation rates of 0.36, 1.45, 1.56 and 3.37 copulations/12 hrs during the 4 weeks following immigration. In contrast, neither of two males (RB and RM) from which we have pre-emigration, but not postimmigration focal samples were observed to copulate during the 4 weeks before emigration. Difficulties of individual recognition of unmarked males precluded calculation of immediate postimmigration mating success for them. However, lumping focal observations for unmarked adult males gives a rate of 0.76 copulations/12 hours, more than twice the median for all marked males (Table I). Since most of these males were unmarked because they had newly immigrated, this again suggests that immigrating males often mate at high rates.

High mating success might be realized when the new male asserts himself following a series of agonistic encounters; the mating behavior of grey-cheeked mangabeys appears to be similar to that of baboons (Hausfater, 1975; Packer, 1979). Each male attempted to maintain close spatial association with a female and tried to prevent other males from getting close to her. Exclusive consortships of one male with a female sometimes continued over an entire estrous period and may have been maintained at night. As in baboons, sometimes there were high levels of aggressive competition for the female, and she would mate sequentially with several males during the estrous cycle. Also as in baboons (Smuts, 1985; Strum, 1987), there appears to be a substantial degree of female choice in mangabeys, which may at least partly determine the strength of the consortship. This is suggested by the lack of close association between the rates of agonistic encounters initiated and of copulations attained by a specific male (Fig. 2). It is also suggested by the fact that females sometimes left the consort male and mated with other males, sometimes including subadults and juveniles, out of view of the consort.

In conclusion, our results strongly suggest that availability of estrous females is an important proximate cause for dispersal in male grey-cheeked mangabeys. Although dispersals might follow increased aggression in a few cases, there is no evidence that dispersal was driven by aggression.

## ACKNOWLEDGMENTS

We thank the Uganda National Council of Science and Technology, Uganda Wildlife Agency, and Makerere University Biological Field Station for permission to conduct the research. Richard Kaserengenyu, John Rusoke, and Clovice Kaganzi provided invaluable help in the field. We thank Richard Howard, Melissa Remis, Kerry Rabenold, Brad Swanson, Maureen McColgin, John Winters and Jamie Skvarla for helpful comments on early drafts of this manuscript. The study was made possible by grant support from the Wildlife Conservation Society, the National Geographic Society, the Rockefeller Foundation, and the Pope Foundation. The research presented here is described in Purdue Animal Care and Use Committee protocol number 95-063 approved on October 11th 1995.

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