

RESEARCH ARTICLE

Changes in Ranging and Agonistic Behavior of Vervet Monkeys (*Cercopithecus aethiops*) after Predator-Induced Group FusionKARIN ENSTAM JAFFE^{1,2*} AND LYNNE A. ISBELL¹¹Department of Anthropology, University of California, Davis, California²Department of Anthropology, Sonoma State University, Rohnert Park, California

Socio-ecological theory predicts that group fusion in female-philopatric primate species will be rare because females experience increased costs by associating with non-relatives. Indeed, fusion has been reported only 14 times in only 4 female-philopatric cercopithecines despite many years of observation. Here, we describe changes in ranging and agonistic behavior of vervet monkeys (*Cercopithecus aethiops*) after the fusion of two groups, the sole group fusion during 11 years of observation, induced by a brief but intense period of apparent leopard predation. Before fusion, both groups made few incursions into the other group's territory and spent most of the time in their own territories. After the fusion, the amalgamated group shifted its activities and used both territories in similar proportion. Rates of female agonism increased after fusion, particularly in the 2 weeks following fusion, and the small group females assumed the lowest ranks in the female dominance hierarchy. Rates of agonism returned to pre-fusion rates a month later. Although rates of high-intensity interactions (i.e., chases) did not increase after fusion, small group females were more likely to be the recipients of, and lose, agonistic interactions than large group females; a small group female and her infant were attacked and wounded by a coalition of large group females shortly after the fusion. The observations presented here reveal that the circumstances surrounding group fusions are more variable than previously realized, but are still in accordance with expectations from socio-ecological theory that predation can favor the formation of larger groups. In this case, under threat of severe predation, individuals may have surrendered group autonomy for the greater security of larger numbers. *Am. J. Primatol.* 72:634–644, 2010. © 2010 Wiley-Liss, Inc.

Key words: dominance hierarchy; female aggression; group size; leopard predation; mortality

INTRODUCTION

Reports of group fusion in female-philopatric primate species are rare, despite many years of observation. Nine cases have been reported in vervets (*Cercopithecus aethiops*) [Hauser et al., 1986; Isbell et al., 1991], one in toque macaques (*Macaca sinica*) [Dittus, 1986, 1987], three in Japanese macaques (*M. fuscata*) [Sugiura et al., 2002; Takahata et al., 1994], and one in yellow baboons (*Papio cynocephalus*) [Altmann, 1980; S. Alberts, personal communication]. According to socio-ecological theory, group fusions should be rare because females in female-philopatric species experience increased costs by associating with non-relatives. For example, females are more likely to be aggressive toward non-kin than to kin and less likely to provide coalitionary aid [Hunte & Horrocks, 1987; Isbell & Van Vuren, 1996; Payne et al., 2003; Silk et al., 2004; Wrangham, 1980]. In addition, transfer into a new group often requires the use of a new and unfamiliar area which can be costly in terms of reduced foraging efficiency and/or increased predation pressure [Isbell & Van Vuren, 1996; Isbell et al., 1990].

When data are available, most of the earlier reports of group fusion in female-philopatric cercopithecines share four characteristics. First, fusion occurs when one group declines to two or fewer adults and a variable number of immatures [Dittus, 1987; Hauser et al., 1986; Isbell et al., 1991; Sugiura et al., 2002; Takahata et al., 1994]. Second, newly immigrant females assume the lowest dominance

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ranks [Dittus, 1987; Hauser et al., 1986; Sugiura et al., 2002]. Third, although immigrant females are lowest ranking, aggression and harassment of these females is no greater in frequency or severity than that directed toward natal females [Hauser et al., 1986; Sugiura et al., 2002; Takahata et al., 1994; but see Dittus, 1987 for an exception]. Finally, there is a shift in home range use after fusion [Dittus, 1987; Isbell et al., 1990; Sugiura et al., 2002].

Here we describe the conditions surrounding the sole group fusion observed during an 11-year study of a population of vervets in Laikipia, Kenya, and document ranging and agonistic behavior before and after the fusion. We note that there are some similarities between earlier observed fusions and the fusion presented here, i.e., shifts in the ranging behavior of the fused group and the fact that immigrant females assumed the lowest dominance ranks in the fused group. However, there are also differences, including the circumstances precipitating the fusion and the number of adults in the groups that fused.

METHODS

Study Site and Animals

From 1992 to 2002, Isbell and co-workers [e.g., Enstam & Isbell, 2002; Isbell & Pruett, 1998; Isbell et al., 2009; Jaffe & Isbell, 2009] studied a population of vervets on Segera Ranch (36°50'E, 0°15'N, elevation 1,800 m) on the Laikipia Plateau in central Kenya. The vervets lived along the Mutara River. The ecosystem of the Mutara River is typical of riverine habitats elsewhere in Kenya: fever trees, *Acacia xanthophloea*, predominate while smaller understory shrubs and bushes, e.g., *Carissa edulis*, also occur [see Isbell et al., 1998; Young et al., 1997, for more detailed descriptions of the study site].

We studied two groups intensively, designated "large group" ($N = 21$ individuals on the last day observers saw the group intact) and "small group" ($N = 7$ individuals on the last day observers saw the group intact). After these groups fused, the amalgamated group was designated "fused group." In our analysis and discussion of the fused group, we continued to refer to "large group" and "small group" females for consistency, but we considered the small group individuals to be immigrants into the fused group because the first time we located them after the fusion, they were intermingled with the large group in the large group's territory. In addition, during the first three observation days after fusion, the group ranged only in the large group's territory [Jaffe, unpublished data], indicating that the small group individuals were following the large group individuals. All vervets in these groups were individually identified by natural markings and physical characteristics.

Multiple observers recorded all births, deaths, immigrations, emigrations, and disappearances of

vervets during the 11-year study [see Isbell et al., 2009 for details]. Group compositions and birthdates of individuals are listed in Table I. For individuals whose exact day of birth was unknown, we determined the average birthdate from the range of possible dates. In most cases, we knew birthdates to within several days, the exception being NYI, for whom the range was nearly 3 months. We estimated birthdates of the six individuals born before the study began to the nearest year based on body size, presence or absence of elongated nipples, and general appearance (i.e., presence or absence of scars, fullness of pelage), at the beginning of the study.

We classified causes of death following the criteria in Isbell [1990]. Deaths of individuals whose remains were recovered were classified as "confirmed predation." Disappearances of adult females and immatures within 72 hr of being last seen apparently healthy were classified as "suspected predation." Disappearances of individuals who were visibly injured or in poor health before their disappearance were classified as "death by illness." Unweaned infants from 2 months to 1 year of age, who died within 72 hr after their mother's disappearance, were classified as "dying after being orphaned." Observers noted all sightings of predators and their signs (e.g., footprints, claw marks on trees) throughout the study.

This study complied with the American Society of Primatologists' Principles of the Ethical Treatment of Non-Human Primates and protocols approved by the UC Davis Institutional Animal Care and Use Committee (#7124). The study adhered to the legal requirements of Kenya.

Ranging Behavior

From October 5, 1998 to September 1, 1999, KEJ collected data on ranging behavior every 30 min using a Global Positioning System (GPS) unit (Garmin) every observation day (large group: $N = 39$ days, average = 3.2 hr/day, range: 0.5–6.5 hr/day; small group: $N = 22$ days, average = 1.3 hr/day, range: 0.5–4.0 hr/day; fused group: $N = 11$ days, average = 3.6 hr/day, range: 1.5–5.5 hr/day). The GPS had an average error of $15.8 \text{ m} \pm \text{SD } 2.2 \text{ m}$ (range: 12.0–23.5 m, $N = 61$ observation days). The 72 sample days do not include ranging data collected between May 4 and June 21, 1999, because a wildfire occurred on May 4 that affected ranging behavior. For 6 weeks after the fire, individuals in the large group ranged uncharacteristically far from the river into the burned area [Jaffe & Isbell, 2009]. The days that were included in the sampling regimen provided 253 GPS coordinates for the large group, 56 for the small group, and 71 for the fused group. KEJ took GPS coordinates when she was in the center of the group, defined as the location at which she could locate at least half of the group's adult females, with at least one female in each of the general positions to

TABLE I. Group Composition of the Large Group, Small Group, and Fused Group

	Large group on June 1, 1999	Small group on June 16, 1999	Fused group on July 22, 1999 ^a	
Adult and subadult males	BOY (b. 4/93)		–	
	CHI (b. 1/94)		–	
	SHA (b. 12/93)		–	
Adult females		ASP (b. 1992)	ASP	
	DGW (b. 1/95)		DGW	
	FRJ (b. before 1988)		–	
	LCL (b. 2/95)		LCL	
	MOO (b. ~1988)		MOO	
	QSO (b. before 1988)		–	
	SAL (b. before 1988)		–	
	TNC (b. 1/95)		TNC	
		HBN (b. ~1988)	HBN	
		HGL (b. before 1988)	HGL	
Juveniles		BBG (b. 1/95)	BBG	
	CHA (b. 1/98)		–	
	FSH (b. 2/97)		FSH	
	NER (b. 1/96)		–	
	NIN (b. 2/96)		–	
	NYI (b. 12/98)		–	
	RTG (b. 3/95)		RTG	
	SIN (b. 1/96)		SIN	
	SWA (b. 2/98)		SWA	
	TMY (b. 3/97)		TMY	
		SAM (b. 1/96)	SAM	
	Infants	LTO (SAL's infant) (b. 4/99)		–
		OMO (FRJ's infant) (b. 2/99)		–
		IPR (BBG's infant) (b. 7/98)	–	
		MWA (HGL's infant) (b. 4/99)	MWA	

The “large group” and “small group” columns show the composition of the large and small groups on the last date observers saw the groups intact. The “fused group” column shows the members of the large and small groups that formed the fused group. Date of birth shown in parentheses.

^a“–” indicates the individual did not survive to the time of fusion on July 22, 1999.

the north, south, east, and west of herself. Because a group's location at any one time is not independent of its earlier location, we minimized dependence of data by averaging all longitude GPS readings collected on a given day to obtain one longitude reading for that day. We followed the same procedure for latitude readings. The average longitude and latitude readings for each day provide an “average daily GPS point” for that day. We used these average daily data points in our analyses ($N = 39$ daily points for the large group, $N = 22$ for the small group, and $N = 11$ for the fused group).

We determined the territorial boundary ($0^\circ 20.106'N$) between the large group (to the north) and the small group (to the south) by GPS coordinates collected for two intergroup encounters observed by KEJ on March 24, 1999 and May 22, 1999. We corroborated the location of the territorial boundary using descriptions of the location of two other intergroup encounters observed by other researchers on July 13, 1998 and May 29, 1999 in the absence of GPS coordinates. The territorial boundary is drawn in Figure 1 as a straight line

perpendicular to the river and intersecting the two intergroup encounters for which we have GPS coordinates. We defined intergroup encounters as any case in which at least one adult female or juvenile vocalized (intergroup wrrs or chutters) at another group or was physically involved in interactions with females or juveniles of another group. This definition excludes interactions that involved only males, even if they were members of the study groups. Before the fusion, we considered days spent across the territorial boundary as incursions into the territory of the other group. Distance north and south of the territorial boundary between the two groups is based on shortest straight-line distance between the boundary and individual points. Statistical analyses are based on average daily distances from the territorial boundary.

Female Agonistic Behavior and Dominance Hierarchies

Agonistic interactions included approach-avoids, supplants, and chases. The individual who avoided,

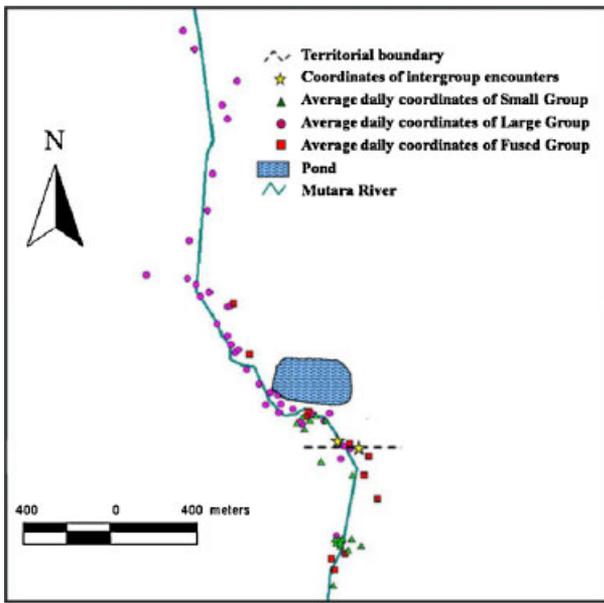


Fig. 1. GIS map showing average daily ranging points for the small group and the large group before the fusion, and the fused group after the fusion. Some points overlap and are not visible on the map. Before the fusion, the large group's territory was north and the small group's territory was south of the territorial boundary.

was supplanted, or was chased (i.e., the recipient) was considered the loser in agonistic interactions. We defined approach-avoids, supplants, and chases following Isbell and Pruett [1998]. We recorded an "approach-avoid" when the recipient cringed, flinched, cowered, or abruptly moved <2 m away from the approacher. We recorded a "supplant" when the approacher replaced the recipient in her exact spot. The resource that was given up during the supplant was also recorded. We recorded a "chase" when the approacher ran toward the recipient, who responded by running away. We consider chases higher-intensity interactions than avoids or supplants because they were more energetic and sometimes involved physical contact between individuals. We analyzed all 39 female-female agonistic interactions involving any of the 8 adult females in the large group, observed by project personnel between October 9, 1997 and July 10, 1999, and all 53 female-female agonistic interactions involving any of the 7 adult females in the fused group, observed by project personnel between July 22 (the latest possible date of the fusion) and December 22, 1999, to determine the female dominance hierarchies of the large group before fusion and the fused group. Because of the small number of interactions in the small group, we included all recorded agonistic interactions ($N = 12$) between the three small group females, observed between the inception of the study in 1992 and July 10, 1999, to construct the dominance hierarchy for the small group. Some of the females listed in the large group

dominance hierarchy died before the fusion and do not appear in the fused group hierarchy. Dominance hierarchies were created and analyzed using MatMan 1.1 (Noldus Information Technology, The Netherlands).

To determine if adult females from the large ($N = 4$) or small group ($N = 3$) won (or lost) agonistic interactions (including chases) more than expected by chance (probability of a win = 0.5), we compared the observed number of wins and losses for individual females from the large and small groups with the expected number of wins and losses, determined by dividing the total number of interactions by the total number of adult females. We also examined the distribution of chases to determine whether adult females from the large or small group were more likely to be the victims of intense aggression after the group fusion. Because of the small number of chases ($N = 12$), we were unable to compare the number of observed and expected chases for individual females as we did for all agonistic interactions. Instead, we compared the total number of chases ($N = 12$) by adult females from the large group and the total number of chases ($N = 0$) by adult females from the small group with the expected number of chases for each group, determined by dividing the total number of chases ($N = 12$) by the total number of females ($N = 7$) and multiplying the result by the number of females in the large ($N = 4$) and small ($N = 3$) groups, respectively.

To avoid potential bias from interobserver differences [see Isbell & Pruett, 1998] for comparisons of rates of agonism, we used data collected only by KEJ during group follows. We examined changes in the rates of agonism before and after fusion. Before fusion, i.e., from October 17, 1997 to July, 15, 1999, KEJ recorded all occurrences of agonism ($N = 16$ and 1, respectively) during 405 hr of observation with the large group (average = 21.3 hr/month, range: 0.9–43.3 hr/month) and 109 hr with the small group (average = 6.2 hr/month, range: 0.5–20.0 hr/month). After fusion, i.e., from July 22 to September 14, 1999, KEJ recorded all occurrences of agonism ($N = 4$) during 31 hr of observation (average = 15.5 hr/month, range: 10.5–20.5 hr/month).

All data (except dominance hierarchies) were imported into the VassarStats statistical computation web site (<http://faculty.vassar.edu/lowry/VassarStats.html>) for analysis. Statistical significance was set at $\alpha = 0.05$ and all tests were two-tailed.

RESULTS

Predation and Decline of Groups over Time

The size of the large group remained relatively stable from 1993 to June 1999 [Isbell et al., 2009]. However, in June 1999, 12 of 21 (57%) members of the large group died or disappeared (Table I). Ten of the twelve (83%) died or disappeared between June 7 and 12 (2 between June 7 and 9, and 8 between June

10 and 12). Two more individuals, a subadult male and an infant, disappeared between June 13 and 16. We recovered the remains of two individuals on June 13, a subadult or adult male and an adult female, who died of confirmed predation. We also recovered the infant's intact remains, and it was classified as having died after being orphaned [see Enstam et al., 2002]. Eight individuals died of suspected predation. The ninth individual was a subadult or adult male, and it is unknown whether he died or transferred to another group. In all, 48% of the vervets in the large group (10 of 21) died of suspected or confirmed predation over the 6-day period between June 7 and 12.

Strong circumstantial evidence suggests that the mortality was caused by leopard(s) (*Panthera pardus*). At this and other study sites, leopards are confirmed predators of vervets [Isbell, 1990; Isbell et al., 2009; Seyfarth et al., 1980; Struhsaker, 1967] and our sightings of leopards or their signs were concentrated around this time. During our 10 observation days with vervets in June 1999, we saw leopards or their tracks in the large group's territory on 40% of those days (leopard tracks on June 12, 13, and 28, and a female leopard and 2 cubs on June 22). By contrast, in the 15 months before the fusion (120 observation days, average = 8 days/month, range: 5–12 days/month), we saw signs of leopards on only 4% of observation days (four sightings/signs in the large group's territory, one in the small group's territory). During the 9-day period when half of the large group disappeared, the group seemed especially agitated. On June 12, for example, the members of the group uncharacteristically scattered and fled upon our approach.

Sometime between June 16 and July 22, one of the small group's 7 members (an infant) disappeared (Table I). We found all seven members of the small group together in their territory for the last time on June 16. They were noted as behaving in an agitated manner. We could not locate the small group between June 16 and 22, although we searched for them repeatedly. On June 22, we found three members of the small group in the large group's territory, but because we could not locate the large group on that day, we do not consider this the date of fusion. We did not relocate the entire small group until July 22. On that day, LAI found the six remaining members of the small group intermingled with the nine remaining members of the large group in the large group's territory. KEJ had found the large group without the small group as recently as July 15, so the fusion must have occurred between July 15 and 22. On July 22, members of both groups were observed to groom one another, and they traveled as a single group (Table I) until the end of the long-term study 2 years later. The one adult male in the small group moved more independently than the rest of the group. We saw him alone on June 13 and once with the large group (but without other

members of the small group) on July 7. He was a natal male of the large group who had transferred to the small group 2 years earlier.

Home Range Use Before and After Fusion

Before the fusion, both groups spent the majority of observation days in their own territories (large group: 90% of 39 days north of the boundary; small group: 73% of 22 days south of the boundary; Fig. 1). After fusion, the group spent a similar number of days in each group's former territory (6 of 11 days south of the boundary and 5 of 11 days north of the boundary; Fig. 1).

Before the fusion, the large group traveled significantly farther north from the territorial boundary (and within its own territory: average = $320\text{ m} \pm \text{SD } 77\text{ m}$, range: 60–980 m) than south into the small group's territory (average = $63\text{ m} \pm \text{SD } 58\text{ m}$, range: 2–212 m, Mann-Whitney U -test: $U = 14.0$, $z = 2.94$, $P < 0.004$; Fig. 2). Similarly, before fusion, the small group traveled significantly farther south of the territorial boundary (and within its own territory: average = $211\text{ m} \pm \text{SD } 55\text{ m}$, range: 38–328 m) than north into the large group's territory (average = $62\text{ m} \pm \text{SD } 79$, range: 41–776 m, Mann-Whitney U -test: $U = 5.5$, $z = 3.1$, $P < 0.002$; Fig. 2). After fusion, however, the fused group's average daily distance north ($142\text{ m} \pm \text{SD } 80\text{ m}$, range: 6–343 m) and south ($172\text{ m} \pm \text{SD } 49\text{ m}$, range: 26–295 m) of the former territorial boundary (Fig. 2) did not differ significantly (Mann-Whitney U -test: $U = 11.0$, $z = 0.64$, $P = 0.5$; Fig. 2).

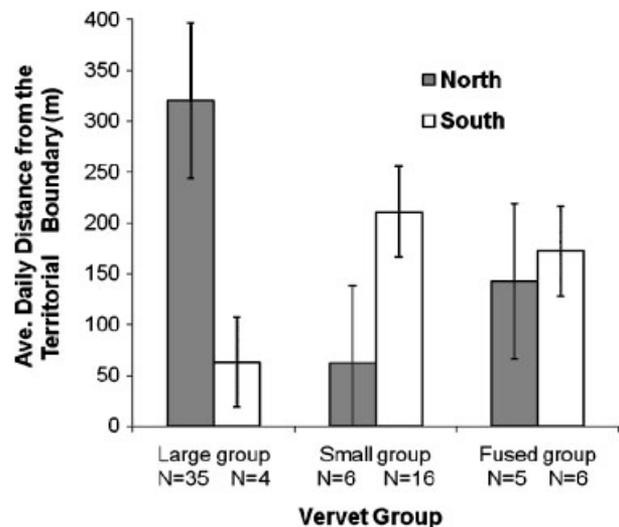


Fig. 2. Average daily distance each vervet group ranged from the territorial boundary between the large and the small group. Before fusion, the large group ranged significantly farther north (into its own territory) and the small group ranged significantly farther south (into its own territory). The fused group ranged the same distance north and south of the former boundary. Number of days each group ranged north and south are indicated directly below each bar. Error bars represent standard deviations.

Female Agonistic Behavior and Dominance Hierarchies Before and After Fusion

Agonistic behavior

Although the number of agonistic interactions in the small group before fusion and the fused group after fusion precluded statistical analysis, the number of agonistic interactions per hour of observation was higher in the 7 weeks after fusion (0.13/hr) than the 19 months before fusion for the large (0.04/hr) and the small (0.01/hr) groups. The increase in the rate of agonistic interactions in the fused group occurred primarily during the 2 weeks immediately after fusion. The rate of agonism between all adult females during these 2 weeks (0.27/hr) was 6 times higher than the large group and more than 20 times higher than the small group before the fusion. By 3–7 weeks after fusion, the rate of female agonism (0.05/hr) declined to a level that was similar to the large and the small groups before fusion.

The 53 agonistic interactions observed after fusion were not distributed evenly across the large and small group females. Twenty-eight percent ($N = 15$) involved a large group female winning an interaction with another large group female, 68% ($N = 36$) involved a large group female winning an interaction with a small group female, and 4% involved a small group female winning an interaction with a small and a large group female once each. During the 5 months after the fusion, the 3 small group females lost agonistic interactions more often than expected (χ^2 goodness of fit = 10.66, $df = 2$, $P < 0.005$), whereas the 4 females from the large group won agonistic interactions more often than expected (χ^2 goodness of fit = 24.31, $df = 3$, $P < 0.001$). Although females from both large and small groups were chased as much as expected ($N = 4$ and 8, respectively) during the 5 months after the fusion (χ^2 goodness of fit = 2.14, $df = 1$, $P = 0.14$), large group females chased other females more than expected ($N = 12$, χ^2 goodness of fit = 6.94, $df = 1$, $P > 0.008$), whereas small group females never chased other females.

Although the number of high-intensity interactions (i.e., chases) vs. low intensity interactions (i.e., supplants and avoids) did not differ significantly (before fusion: 13 high and 26 low intensity in the large group; after fusion: 12 high and 41 low intensity, $\chi^2 = 0.81$, $df = 3$, $P = 0.37$), and the proportion of high-intensity interactions actually *decreased* after fusion (33% before vs. 23% after), the intensity of 1 observed interaction was greater than any other female interaction observed during the 11-year study.

At 08:40 on August 1, KEJ found adult females MOO (from the large group) and HGL (from the small group) grooming each other in an *A. xanthophloea* tree. HGL had her 2-month-old infant with her. At 09:05, KEJ heard several adult females and juveniles chattering, and shortly after, two adult females (TNC and DGW, both from the large group) climbed toward MOO and HGL. TNC, DGW, and MOO then chased HGL and her clinging infant through the tree, biting her on the tail and back. When they reached the end of a branch, one of the attackers grabbed HGL as all three females bit her and her infant. When the unidentified female let go, HGL dropped, with her infant, approximately 12 m to the ground and ran into some bushes. After the agonistic interaction, the three attackers, all from the large group, groomed each other. Seventy minutes later, KEJ located HGL and her infant in another *A. xanthophloea* tree. Both had wounds on their backs and tails. Eleven days later their wounds were healing but still visible.

Dominance hierarchies

Although the number of agonistic interactions between large and small group females observed before fusion ($N = 39$ and 12 interactions, respectively) precluded statistical analyses to determine the linearity of the hierarchies, we were able to determine female dominance ranks for both groups (Tables II and III).

TABLE II. The Ranked Adult Female Dominance Hierarchy of the Large Group Based on Agonistic Interactions Observed Between October 9, 1997, and July 10, 1999

Approacher (winner)	Recipient (loser)							
	FRJ	LCL	DGW	TNC	SAL	QSO	MOO	BUR
FRJ	*	6	2	0	1	0	3	0
LCL	0	*	5	3	0	1	1	0
DGW	0	0	*	0	3	2	2	0
TNC	0	0	0	*	0	1	2	0
SAL	0	0	0	0	*	0	4	0
QSO	0	0	0	0	0	*	0	0
MOO	0	0	1	0	0	0	*	2
BUR	0	0	0	0	0	0	0	*

*Wins are shown across the columns.

The 53 interactions observed after fusion resulted in a statistically linear dominance hierarchy ($\chi^2 = 42.7$, $df = 23$, $P < 0.02$; Table IV). The dominance ranks of the four large group females (LCL, DGW, TNC, MOO) and the three small group females (HGL, HBN, BBG) alive after the fusion are similar, though not identical, to their ranks before fusion. Before fusion, three of the four large group females (LCL, DGW, TNC) held ranks near the top of the hierarchy. After fusion, all four large group females kept their ranks relative to one another, except DGW, who reversed ranks with LCL (see Tables II and IV). The small group females also kept their ranks relative to one another. However, HGL, the highest ranking female in the small group before fusion, became the third lowest ranking female in the fused group dominance hierarchy (Tables III and IV).

DISCUSSION

As mentioned in the Introduction, earlier reports on group fusion in female-philopatric cercopithecines share, to some degree, four traits. Our observations on the circumstances surrounding the one group fusion in an 11-year study of vervet monkeys in Laikipia are similar in many ways to earlier reports, but differ in some respects.

TABLE III. The Ranked Adult Female Dominance Hierarchy of the Small Group Based on Agonistic Interactions Observed Between 1992 and July 10, 1999

Approacher (winner)	Recipient (loser)		
	HGL	HBN	BBG
HGL	*	8	2
HBN	0	*	2
BBG	0	0	*

"Wins" are shown across the columns. Only females that were alive at the time of fusion are included.

TABLE IV. The Ranked Adult Female Dominance Hierarchy of the Fused Group Based on Agonistic Interactions Observed Between July 22 and December 22, 1999

Approacher (winner)	Recipient (loser)						
	DGW	LCL	TNC	MOO	HGL	HBN	BBG
DGW	*	0	1	3	1	4	1
LCL	0	*	5	0	3	5	4
TNC	0	1	*	5	3	2	6
MOO	0	0	0	*	3	1	3
HGL	0	1	0	0	*	0	1
HBN	0	0	0	0	0	*	0
BBG	0	0	0	0	0	0	*

"Wins" are shown across the columns.

Number of Adults at Fusion

The relatively large number of adults in both groups ($N = 4$ in each group) that we observed in Laikipia at the time of fusion (Table I) has not been reported for any other group fusion [i.e., Dittus, 1987; Hauser et al., 1986; Isbell et al., 1991; Sugiura et al., 2002; Takahata et al., 1994]. The unusual circumstances precipitating the fusion may explain our anomalous results. The Laikipia vervet groups fused within a month after an exceedingly rapid decline in group size caused mainly, if not entirely, to leopard predation. In other reports, group fusion was precipitated by a slow decline in group size attributed to a reduced birth rate rather than an increased mortality rate [Sugiura et al., 2002; Takahata et al., 1994]. Even in the Amboseli National Park, Kenya, where leopard predation immediately precipitated many fusion events [Isbell et al., 1991], fusions were also preceded by a slow decline in group size as a result of gradual habitat degradation [Cheney & Seyfarth, 1990; Isbell, 1990; Struhsaker, 1973, 1976]. The exception to these observations is Dittus' [1987] description of more abrupt group size decline before fusion in toque macaques, in which two females and their dependent offspring died a month before the remaining adult female and four juveniles transferred into a neighboring group.

Earlier reports on group fusion, including reports of fusion in the Amboseli vervets, suggested that the primary benefit of group fusion is enhanced intergroup competition that accompanies being part of a larger group [Dittus, 1987; Hauser et al., 1986; Isbell et al., 1991; Sugiura et al., 2002; Takahata et al., 1994]. This explanation hinges on the idea that larger groups can and do supplant smaller groups from resources [e.g., Cheney & Seyfarth, 1987; Dittus, 1987; Hood & Jolly, 1995; Isbell et al., 1990; Robinson, 1988; Wrangham, 1980]. In all the earlier reports on group fusion, immigrants were members of a group that became exceedingly small (e.g., $N < 5$ individuals), with only one or two adults. In such cases, it is hypothesized that the remaining

individuals are unable to effectively defend their home range and compete successfully for resources [e.g., Hauser et al., 1986; Isbell et al., 1991; Sugiura et al., 2002], necessitating fusion with a neighboring group.

Intergroup competition does not seem to explain the group fusion in Laikipia, however. Even though the large group was three times the size of the small group ($N = 21$ and 7 , respectively) before fusion, intergroup encounters were rare. Although the few intergroup encounters we observed were invariably won by the large group [Isbell, unpublished data], the ranging behavior of both groups reveals that they largely attempted to avoid one another (Fig. 1). There appeared to be no effort by the large group to move into the small group's territory. Moreover, it is not clear how intergroup competition could be a factor when the fusion occurred only after both groups became more symmetric in size.

A more plausible explanation is predation avoidance, which has long been considered a factor in maintaining large group sizes [e.g., Alexander, 1974; Busse, 1977; Hill & Lee, 1998; Miller, 2002; van Schaik, 1983; but see Miller & Treves, 2007]. Although vervets do not engage in cooperative defense against predators because of their small size [Cheney & Wrangham, 1987; Miller & Treves, 2007], they may be able to reduce the cost of predation to themselves through dilution or reduce the frequency of attack through enhanced predator detection if they live in larger groups [e.g., Alexander, 1974; de Ruiter, 1986; Isbell & Young, 1993; Miller, 2002; Pulliam & Caraco, 1984; van Schaik, 1983; van Schaik et al., 1983]. In Laikipia, the one group fusion occurred after the large group declined to its smallest size during the entire 11-year study [Isbell et al., 2009], when nearly half the individuals were lost over a very short period of time as a result of suspected or confirmed leopard predation. The large group was highly agitated during this time. Although the small group was not as severely reduced in size, they were also visibly agitated. We suggest that the extraordinarily high predation rate provided the impetus for the fusion of the two groups. By fusing, each group roughly doubled in size, which would have increased the number of individuals available to search for predators [Isbell & Young, 1993; van Schaik et al., 1983]. In the Amboseli vervet groups, each additional individual added, on average, at least 0.18 scanners per unit time [Isbell & Young, 1993]. Large group size may be especially beneficial when predation pressure is reliably intense or unrelenting, as was the case before the fusion reported here. It is perhaps notable that after the fusion, disappearances ceased until 6 months later when 3 individuals were killed in their sleeping tree by leopards, and then ceased altogether until the study ended [Isbell et al., 2009].

Rank of Immigrant Females After Fusion

As with earlier reports, our observations on group fusion in the Laikipia vervets indicate that the small group females assumed the lowest ranks in the fused group's dominance hierarchy after they transferred (Table IV). In most other cases of fusion, a single female (and variable numbers of juveniles) transferred into another group, and the low dominance rank of those females was suggested to result from a lack of adult allies in the new group [Sugiura et al., 2002]. This does not adequately explain the low dominance rank of the small group females in this case, however, because unlike all other reports of group fusion in female-philopatric cercopithecines, our fusion occurred when there were at least three adult females in each group. Despite potential allies accompanying them into the new group, in the 5 months after the fusion, small group females were the recipients of agonism from large group females in two-thirds of all interactions. A possible reason for this asymmetry is that three of the four large group females were already high-ranking before fusion. Moreover, the small group females may have been somehow less competitive in agonistic interactions, either relative to the large group females or independent of them. One indication of the latter might be seen in their very low rate of agonistic interactions before the fusion (Table III).

Frequency and Severity of Aggression After Fusion

Unlike most other reports on group fusion, in which immigrant females do not suffer greater frequency or severity of aggression than natal females, in the 7 weeks after our group fusion, agonistic interactions did increase (from 0.04/hr in the large group and 0.01/hr in the small group before fusion to 0.13/hr after fusion). However, this increase was not spread equally between small group and large group females. Small group females were the aggressors in only two of 53 interactions. Of the 51 interactions in which large group females were the aggressors, 36 of these (71%) involved small group females as the recipients of agonism. Thus, the increase in agonism after fusion was due primarily to agonistic behaviors directed at small group females by large group females. In addition, the rate of agonism was highest during the 2 weeks after the fusion, and declined by 3–7 weeks after fusion to levels observed in both groups before fusion. In toque macaques, Dittus [1987] also found increased rates of agonism immediately following group fusion, that the majority of agonism was directed at the females who immigrated into the fused group, and that the rates of agonism declined rapidly. Higher rates of agonism shortly after the introduction of unfamiliar individuals to a group are not unusual. Increased rates of agonism directed at immigrant males are

common in most mammalian species even though male dispersal is the norm [Isbell & Van Vuren, 1996]. Thus, the heightened rates of agonism recorded in the first weeks after fusion may indicate that females were establishing rank relations among themselves. It is possible that other observations of group fusion in female-philopatric cercopithecines [Hauser et al., 1986; Sugiura et al., 2002; Takahata et al., 1994] did not detect higher rates of agonism initially after fusion because data were not collected immediately after the fusion event. A lag in observations immediately after a fusion event may mean that observers miss initial bouts of agonism, making it seem as though no heightened agonism took place.

Like all other reports of group fusion, however, the *overall intensity* of agonistic interactions (as measured by the number of chases vs. other agonism) did not increase after fusion. In fact, the proportion of high-intensity interactions decreased by 10% after fusion. Our observations indicate that brief but severe aggression can nonetheless be directed against immigrant females, especially in the days immediately following fusion. Shortly after the fusion, three adult females from the large group attacked and wounded a female and her infant from the small group. Although the female and her infant survived, intergroup encounters in other female-philopatric cercopithecines have been accompanied by lethal aggression [*C. diana*: McGraw et al., 2002; *C. mitis erythrarchus*: Payne et al., 2003].

The most severe aggression we observed after the Laikipia fusion was directed toward HGL, the only female in the combined group with a young infant. Infants are often highly attractive [e.g., Brent et al., 2008; Hrdy, 1976; Isbell, 2008; Manson, 1999; Silk, 1999; Silk et al., 2003; Stanford, 1992], especially when they are young [i.e., <2 months of age: Gumert, 2007; Nicolson, 1987]. In the Amboseli vervet fusions, Hauser et al. [1986] found that immigrant females held and groomed the infants of natal females at similar or higher rates compared with natal females, perhaps as a means to accelerate their integration into the group. However, unlike Amboseli vervets, the only female in the fused group to have an infant was a member of the small group. Although immigrant females may use allomothering of natal females' infants to hasten their acceptance as a group member, infant handling may be a form of harassment when directed at immigrant females by natal females. In the toque macaque fusion described by Dittus [1987], the sole adult immigrant female had a dependent offspring. In the first few weeks after fusion, the dominant female of the natal group handled the infant more than any other female (except the mother) and was observed pulling the infant's head from the mother's teat, preventing nursing. The infant died a month after the fusion.

It is conceivable that the attention directed at HGL and her infant by MOO before the attack on

August 1, 1999 was not a form of affiliative behavior, but harassment. HGL was low-ranking and the only female with a young infant, conditions that have been identified as inciting harassment or kidnapping in other species [Altmann, 1980; Hrdy, 1976; Isbell, 2008; Nicolson, 1987]. Because we had difficulty locating the fused group during the last 15 days of July, potential harassment of HGL's infant could have also occurred before August 1, similar to the pattern of behaviors observed by Dittus [1987]. The primary difference between the two situations, however, is that in the toque macaques the infant's mother apparently allowed her infant to be handled by the higher-ranking natal female, whereas in our case HGL may have attempted to keep her infant from other females. This, in combination with the fact that HGL was a recent immigrant, the only female with a dependent infant, and low ranking, may have amplified the aggression against her.

Change in Ranging Behavior After Fusion

As with toque [Dittus, 1987] and Japanese macaques [Sugiura et al., 2002] and vervet monkeys in ANP [Isbell et al., 1990], the group fusion in vervets in Laikipia was accompanied by a shift in home range use. Before fusion, both groups actively avoided the other group's territory and made relatively few incursions across the territorial boundary (Fig. 1). After fusion, the combined group shifted its ranging and traveled similar distances north and south of the former boundary (Fig. 2). A primary benefit of home range shifts is increased access to resources over time [Dittus, 1987; Isbell et al., 1990]. However, in the short run, foraging efficiency may decrease because females may not be familiar with the location of feeding sites [Isbell & Van Vuren, 1996]. Females need not suffer reduced foraging efficiency, however, if they can rely on others who are familiar with the area to lead them to food sources. As with toque macaques [Dittus, 1987], who often followed the immigrant female to feeding sites in her former home range, large and small group female vervets in Laikipia may have also benefited from the knowledge of their new group mates when ranging in unfamiliar areas.

Although we expected the larger group to determine the ranging behavior of the combined group (as occurred in Amboseli), it is unclear why the fused group spent so much time in more dangerous area near and north of the pond [as evidenced by more leopard sightings, disappearances, and recovery of remains in that area; Isbell & Jaffe, unpublished data]. One possible explanation for this pattern is that site fidelity, even after heavy predation, may be based on a simple (and usually reliable) rule that familiar areas are always safer than unfamiliar areas. Evidence from the ANP suggests that vervets may increase their vulnerability to

predators when they move into new areas and that the risk remains high until individuals spend sufficient time in those new areas [Isbell et al., 1990, 1993].

Because group fusion has been documented only 14 times in 4 species of female-philopatric cercopithecines [baboons: Altmann, 1980; toque macaques: Dittus, 1986, 1987; vervets: Hauser et al., 1986; Isbell et al., 1991; Japanese macaques: Sugiura et al., 2002; Takahata et al., 1994], any observations related to this phenomenon greatly enhance our understanding of it. The observations presented here suggest that the circumstances surrounding group fusions are more variable than previously realized. In addition to occurring in response to asymmetry in intergroup competition, we suggest that fusions can occur in response to extraordinarily heavy predation, causing animals to surrender group autonomy for greater safety through larger numbers, despite increased aggression immediately after fusion.

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