

# Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank

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## Summary

A common practice in studies of social animals is to rank individuals according to dominance status, which has been shown to influence access to limited resources and stability of social relationships, and may in turn correlate with reproductive success. According to the socioecological model for primates, most female dominance relationships are either nepotistic or virtually undetectable (egalitarian), with nepotistic species being philopatric, and dispersing females being egalitarian. Female mountain gorillas (*Gorilla beringei beringei*) disperse, and they have been characterized as being egalitarian, but previous studies have not examined their dominance relationships from a long-term perspective. We evaluated 15 matrices of displacement/supplantation interactions that spanned 30 years of observations in the Virunga Volcanoes region, and included 51 female mountain gorillas in six groups. Only 4% of displacements were directed against higher ranking females, and when matrices had less than 5% unknown dyads, linearity indices were consistently greater than 0.95. Therefore, previous results suggesting undetectable dominance relationships may have reflected an insufficient quantity of data for this species, rather than actual nonlinearity in its hierarchies. Dominance depended on age and group tenure rather than nepotism, yet some females maintained a high ranking for most of adulthood (15–25 years). Most rank shifts occurred through changes in group composition, rather than switches in established relationships. These results fit within growing evidence for linear individualistic hierarchies in some primates, often coupled with dispersal, as commonly found in ungulates. In light of these results, we propose that the dominance relationships of female mountain gorilla are best characterized as ‘Dispersal-Individualistic’ instead of the previously suggested ‘Dispersal-Egalitarian’.

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## **Introduction**

A common practice in studies of social animals is to rank individuals according to dominance status, which has been shown to influence access to resources and stability of social relationships. Dominance has been defined as “an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favor of the same dyad member, and a default yielding response of its opponent rather than escalation” (Schjelderup-Ebbe, 1922; Drews, 1993). If animals can predict the outcome of agonistic encounters, through assessments of morphological traits, displays, or previous experience with individuals they recognize, then they may try to avoid conflicts where they have little chance of success (Drews, 1993). Thus, social dominance may reduce the level of aggression in a group and the associated risk of injury (Hand, 1986; de Waal & Luttrell, 1989). If dominance rank positively correlates with access to limited resources, high ranking individuals should obtain greater reproductive success than low ranking individuals.

The pattern of dominance relationships exhibited by a species may depend on one or more underlying causes: (1) Individual traits, such as body size or fighting ability (Clutton-Brock et al., 1979). (2) Age and/or tenure, where rank may increase with age and be maintained even when individuals are no longer in their prime because of winner/loser effects (e.g., Beacham, 2003). Adults will impose dominance on younger individuals while they still have a size (trait) advantage so they can maintain dominance once sizes become similar (Thouless & Guinness, 1986; Coté, 2000). (3) Nepotism, where rank is determined largely through coalitions within matriline, with daughters ranking below their mother (Walters & Seyfarth, 1987; Mori et al., 1989; Holekamp et al., 1996). (4) Reproductive value, which is highest near age of first parturition, so an inverse-age pattern develops (Borries et al., 1991; Combes & Altmann, 2001).

According to the socioecological model, the distribution and abundance of food resources will determine the type of social relationships among female primates, including dominance relationships (Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997). When food is distributed in high-quality

patches that are too small to accommodate all group members, females exhibit within-group contest competition, philopatry, nepotism, and strong formalized dominance relationships that can be used to create hierarchies. Isbell & Young (2002) propose that dominance relationships may be considered 'strong' when they are expressed frequently (high rate of interactions), when they are imposed decisively (few interactions with subordinates prevailing), and when they are maintained for a substantial portion of reproductive lifespans (temporal stability).

When food is evenly distributed, contest competition may be rare or absent and scramble competition usually prevails. Nepotism becomes less important, which allows for female transfers (Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997). Dominance hierarchies are expected to be nonexistent or weak and unstable in such cases, mainly based on individual competitive abilities, and often correlated with age (Dunbar, 1988; Sterck & Steenbeek, 1997). Dominance relationships may be considered 'weak' when females do not form clear linear hierarchies, but classical measures to test if hierarchies show statistically significant linearity may also be sensitive to other factors such as group size and the quantity of data available (Koenig, 2002; Galimberti et al., 2003).

Mountain gorillas do not face appreciable contest competition, because they feed on abundant, evenly-distributed herbaceous vegetation (Watts, 1984, 1985). They are classified as being 'dispersal egalitarian' according to the socioecological model (Sterck et al., 1997). Dominance relationships among female mountain gorillas have been characterized as 'weak or unclear' for several reasons (Stewart & Harcourt, 1987; Watts, 2001). First, their dominance hierarchies based on approach-retreat interactions (displacements and avoidances) have not consistently shown significant linearity (Harcourt, 1979a; Watts, 1985, 1994; Harcourt & Stewart, 1987, 1989; Stewart & Harcourt, 1987). In addition, their female dominance relationships do not involve ritualized signals of submission, such as the pant grunts of chimpanzees (Wittig & Boesch, 2003) or bared teeth displays of macaques (Sterck & Steenbeek, 1997) as an indication of 'formal' dominance (de Waal & Luttrell, 1989). Females often make a 'grumble' vocalization as an apparent signal of submission to silverbacks, but they rarely grumble after receiving aggression from other females (Watts, 1994). Indeed, females rarely respond submissively to any aggression from other females; their most common responses are to ignore it or to retaliate; and they could not be ranked linearly when using all agonistic interactions (Watts, 1994).

Perhaps due to their apparent weakness, the female dominance relationships of mountain gorillas have not been assessed from a long-term perspective. Yet even weak dominance relationships have been shown to significantly influence reproductive success in some species when examined over the long term (Hanuman langurs: Borries et al., 1991; chimpanzees: Pusey et al., 1997). Long-term studies can help to evaluate the adaptive significance of dominance, through its influence on lifetime reproductive success. For example, if each female holds a wide range of ranks throughout adulthood, any advantages she gains while dominant may be offset by the disadvantages from when she was subordinate (Gouzoules et al., 1982; Alados & Escos, 1992; Coté, 2000). While several studies have examined long-term dominance relationships of species that exhibit female philopatry (e.g., baboons: Hausfater et al., 1982; Samuels et al., 1987; Combes & Altmann, 2001), the chimpanzee study (Pusey et al., 1997) represents the only long-term analysis of a primate in which females disperse.

To examine long-term dominance relationships in female mountain gorillas, we evaluated 15 matrices of supplantation/displacement interactions that include 51 females from six groups of mountain gorillas in the Virunga Volcanoes region (situated on the border of Rwanda, Uganda, and Democratic Republic of Congo), using intermittent observations from 1971-2001. First we present the classical linearity measures for hierarchies derived from those matrices, and we evaluate the extent to which they may reflect the actual strength of dominance relationships. We assign ordinal ranks to each female in the hierarchies, using one of the most widely recognized methods (inconsistency and strength of inconsistency, de Vries, 1998). Next, we examine proximate factors which could influence dominance relationships: age, group tenure, whether the female is in her natal group, and the rank of her mother (if present). Lastly, we calculate how frequently females shifted ranks through changes in group composition (births, deaths, immigrations, emigrations, group fissions) versus dominance switches among established females. We discuss these results within the context of the socioecological model and other underlying factors that may shape the patterns of long-term dominance relationships, and the potential impact on lifetime reproductive success.

## Methods

### *Data collection*

Data were collected from several groups that have been habituated for over 30 years by the Karisoke Research Center (Table 1). Some groups were evaluated repeatedly, and studies continued after a few group transitions. When Group 4 disintegrated in 1978, its females joined Nunkie's group. When Nunkie's group disintegrated in 1985, its females joined the newly formed Beetsme's group. Group 5 fissioned in 1993 to form Shinda's group and Pablo's group (see Robbins, 2001 for details of group changes). The new and previously published data came from a combination of focal and ad libitum observations of approach-retreat interactions (displacements). A displacement is defined as when "one female made a non-aggressive approach to a second, stationary female, who watched the approacher and, when the approacher was within 2 m, moved more than 2 m farther away" (Watts, 1994).

Unpublished data are derived from the long-term behavioral records of the Karisoke Research Center, which were collected by the majority of researchers and research assistants working at Karisoke from 1980-2001. Data from 2-3 years of observations were combined into each matrix. Long evaluation intervals were needed due to low displacement rates (Watts, 1985), and because displacements were predominantly recorded on an ad libitum basis by observers conducting other research projects. While the research groups have been monitored nearly continuously since the late 1960's to ensure accurate demographic records, there are some gaps in the behavioral data collection, with the most noticeable gap being from 1993-1999 due to political instability in the region.

To evaluate the hierarchies on a consistent basis, we included only females who had become adults by the end of a study interval. Adults are defined as all females who have reached 6 years of age, which includes the 'subadult' classification that is typically applied to females from 6-8 years old, and the 'young adult' classification for females 8-12 years old (e.g., Williamson & Gerald-Steklis, 2003). About 20% of the females were first observed as subadults or young adults, and their estimated age is reportedly accurate to within at least 2 years (Gerald, 1995). Another 10% were first observed as 'mature' adults, with an estimated age of  $16 \pm 4$  years. Only three (5%) were first observed as 'elder' females, with an estimated age accuracy of  $\pm 10$

**Table 1.** Statistical summary of dominance matrices. Asterisks indicate the matrices that were included in the smaller dataset for meta-analysis. Unknown dyads have no displacements between the two females. Upward displacements are the displacement of a higher ranked female by a subordinate.  $K$ ,  $h$  &  $h'$  are linearity indices, ranging from 0 (random) to 1 (linear). PLC is the probability that linearity is due to chance. References: a) Harcourt, 1979; b) Watts, 1985; c) Harcourt & Stewart, 1989; d) Watts, 1994; e) this report.

Matrix	Group	Years	Females	dyads		displacements		$h$	$h'$	$K$	PLC	refs
				total	unknown	total	upward					
1*	g4	1971-72	5	10	10%	30	0%	0.950	1.000	0.950	0.121	a
2	g4	1978	5	10	0%	65	2%	1.000	1.000	1.000	0.116	b,d
3*	nk	1981-83	6	15	7%	48	23%	0.771	0.800	0.750	0.081	c
4*	bm	1988-89	7	21	0%	94	2%	0.982	0.982	0.982	0.002	e
5	bm	1990-92	7	21	0%	92	2%	0.982	0.982	0.982	0.003	e
6	bm	1999-2001	8	28	36%	40	3%	0.429	0.548	0.400	0.198	e
7*	g5	1972-73	7	21	52%	34	0%	0.500	0.696	0.500	0.115	a
8	g5	1978-79	7	21	33%	26	15%	0.321	0.446	0.321	0.448	b
9	g5	1982-83	6	15	7%	39	3%	0.800	0.829	0.781	0.084	e
10	g5	1984-85	11	55	7%	112	0%	0.955	0.973	0.955	0.000	d
11	g5	1986-87	12	66	2%	132	2%	0.993	0.997	0.993	0.000	d
12	g5	1988-89	11	55	20%	110	3%	0.573	0.623	0.573	0.005	e
13	g5	1990-92	15	105	56%	98	5%	0.270	0.375	0.270	0.038	e
14*	sh	1999-2001	7	21	38%	20	0%	0.589	0.732	0.589	0.088	e
15*	pb	1999-2001	17	136	65%	80	8%	0.143	0.251	0.143	0.149	e

years; they each appear only once or twice in the hierarchies from the earliest years of the study. Almost 65% of the females were observed shortly after their birth, so their ages are known to well-within one year, and the identity of their mother is known too (ibid). We consider kinship relationships here to include only mother-daughter relationships known from the long term demographic records.

### *Dominance calculations*

We used Matman software (Noldus, 1998), to calculate the linearity indices of Kendall ( $K$ ) and Laudau ( $h$ ), and an adjusted Laudau index ( $h'$ ) that is corrected for the number of 'unknown' relationships (i.e., dyads with no interactions) (de Vries, 1995). All three indices increase from 0 to 1 as a hierarchy improves from random to completely linear. Linearity in a set of binary dominance relationships depends on the number of established relationships and on the degree to which these relationships are transitive. If for every pair of animals, A and B, either A dominates B or B dominates A and if for every three animals A, B and C in the group, A dominates B and B dominates C implies A dominates C, then there is perfect linearity in the set of dominance relationships. The individuals can then be ranked into a fully linear hierarchy. When some triads form circular triangles and/or when some dyads have an unknown or tied relationship the degree of linearity decreases (de Vries, 1995).

We also used Matman for each matrix and observation period to calculate 'PLC', the probability that linearity occurs by chance (see de Vries, 1995; 1998 for details of all four linearity calculations). Using the results from all 15 matrices, we performed stepwise linear regressions to examine how  $K$ ,  $h$ ,  $h'$  and PLC depended upon the number of female dyads in a matrix, the number of displacements observed, the number of unknown dyads, and the number of years in an evaluation interval. Additionally, to integrate the individual statistical analysis results we combined the PLC values from all the matrices using a meta-analysis (Fisher transformation: Sokal & Rohlf, 1995, page 795) to determine an overall probability of linearity. To avoid pseudoreplication, we also performed the meta-analysis using only the first matrix from each group. About 30% of all dyads were evaluated at least twice in the complete dataset, but less than 1% appeared repeatedly in this smaller dataset.

We also used Matman to determine ordinal dominance rankings for each female within each hierarchy. Matman uses the I&SI method (de Vries, 1998), which involves iterative calculations that first minimize the number of inconsistencies (I) in a dominance matrix, and then minimize the strength of those inconsistencies (SI) subject to the condition that 'I' does not increase (de Vries, 1998). An inconsistency is defined as any dyad in which the lower ranked individual wins the majority of decided encounters. The strength of an inconsistency is the absolute difference between the ranks of the two individuals involved. The I&SI method ranks individuals into a linear hierarchy, and deVries (1998) warns that the predicted rankings of hierarchy may only be valid if the linearity is statistically significant.

In addition to the ordinal dominance rankings, for analyses we also used standardized ranks and broad classifications. We standardized the I&SI rankings using Equation 1:

$$\text{Standardized rank} = (N - R)/(N - 1) \quad (1)$$

Where  $R$  is the ordinal rank to be standardized, and  $N$  is the number of females in the matrix. The standardized rank of each female equals the proportion of other females who are below her in the matrix, so the lowest female in each matrix has a standardized rank of 0, and most dominant female has a standardized rank of 1 (see Rhine et al., 1989; Coté, 2000 for similar approaches). Females were also divided into 'high' or 'low' rank classifications for each hierarchy. When an uneven number of females was present, the median ranking female was assigned as high-ranking (van Noordwijk & van Schaik, 1999).

### *Potential factors affecting dominance*

We performed multiple regressions to determine how standardized rank correlates with the age (and age<sup>2</sup>) of each female, the length of her tenure in the group, whether she was in her natal group (no = 0, yes = 1), and the standardized rank of her mother if present (and 0 if the mother was not present). To reduce pseudoreplication we again performed the regression using data from only the first matrix of each gorilla group. The 'age' variable may reflect whether rank depends upon individual experience or reproductive value, and the age<sup>2</sup> variable could reflect any nonlinearities in such trends. The age<sup>2</sup> variable may also reflect whether rank declines at advanced ages, as might be

expected for past-prime females if dominance depends upon individual traits. The variable for mother's rank may reflect nepotism, since daughters usually rank below their mother in such hierarchies. The variables for group tenure and natality may reflect any influence of relationships with other group members (Scott & Lockard, 1999).

The rank of a female cannot depend solely on her own values for those variables (age, group tenure, natality, and mother's rank); it will also depend upon the values for the other females in her group. For example, even a very young female may have top rank, if she happens to be in a group with females who are even younger. Therefore, in addition to doing the regressions using rank as the dependent variable, we also used an approach based on calculations by Tufto et al. (1998) to predict how the winner of each dyad is determined by values for both individuals involved. By focusing on dyads, this approach transcends the question of whether a dominance hierarchy is linear. In fact, it even explains how circular hierarchies could be expected to arise when winning depends on at least two traits and interactions between them (Tufto et al., 1998). Tufto et al. (1998) used a maximum likelihood method to estimate the probability  $p_{jk}$  that an individual 'j' will win any given encounter with another individual 'k':

$$\text{logit } p_{jk} = a^*(x_j - x_k) + b^*(y_j - y_k) \dots \quad (2)$$

where  $x$  and  $y$  are traits of the individuals  $j$  &  $k$ , and  $a$  &  $b$  are regression constants. For example,  $p_{jk}$  could represent the probability that female 'j' will displace female 'k', expressed as a percentage of the total number of displacements between the two females. Her winning probability ( $p_{jk}$ ) could depend upon the difference between their ages ( $x_j - x_k$ ), where  $x$  signifies the age of each female, and the difference between their group tenures ( $y_j - y_k$ ), where  $y$  signifies the group tenure of each female. The full set of independent variables in our analysis was again the age (and age<sup>2</sup>) of each female, her tenure in the group, whether she was in her natal group ('natality'), and the rank of her mother if present. To avoid pseudoreplication we randomly chose one data point for each female pair from among all of their decided dyads in the matrices.

Unlike the I&SI method, the Tufto analysis involves an underlying assumption that each dyadic interaction is independent of every other dyadic interaction. This assumption is not valid if some individuals interact preferentially with others, or if the outcome of one interaction affects the probability for future interactions (e.g., de Vries, 1998; Gammell et al., 2003). To

partially address this issue, we modified the Tufto approach by performing a logistic regression which merely used the overall winner in each dyad at each time (i.e., the dependent variable was 0 when individual 'j' lost, and 1 when she won). But as Gammell et al. (2003) suggested, every dominance ranking method has its limitations, so the results of any one method may not fully reflect all of the underlying aspects of the dominance relationships being studied.

### *Potential pathways for rank changes*

We performed additional analyses that focused on the dyads that recurred in more than one matrix, to calculate how frequently the winner remained the same from one evaluation to the next. We also examined the frequency of rank switches with recurring evaluations between the same two individuals. We define a rank switch as each instance in which the dominant female in the former evaluation was subordinate in the latter evaluation. When a new female entered a hierarchy, we did not count her as switching ranks with those below her, or as being switched by those above her. Note that we avoid the term 'reversals' which has been used to describe both rank switches in overall dominance relationships and single instances when a subordinate displaces a more dominant female. We use the term 'upward interactions' to describe those isolated displacements against the hierarchy.

When a female was evaluated repeatedly, we counted how frequently her dominance classification changed between 'high' and 'low'. When she remained in the same group for two successive evaluations, we calculated average values for her rank in the former and latter matrices, and the number of rank switches that she underwent with other females above and below her. We also calculated the average number of females who left the former hierarchy through death or emigration, and the average number of immigrations and newly matured females in the latter matrix. We calculated the average rank of immigrants and emigrants, and we reviewed the effects on rank of one group fission.

## **Results**

### *Dominance calculations*

Linearity indices ranged from 0.14 to 1.00, with a median value of 0.77 (Table 1). The PLC ranged from <0.001 to 0.45, with a median value of 0.084.

**Table 2.** Statistical summaries from stepwise regressions for linearity measures ( $h$ ,  $h'$ ,  $K$ , and PLC) versus the number of displacements observed, the number of dyads, and the percentage of unknown dyads in each matrix.

Dependent variable	Significant independent variable(s)	$R^2$	df	F-ratio	$p$
$K$	%unknown dyads	0.857	13	77.83	<0.001
$h$	%unknown dyads	0.869	13	84.61	<0.001
$h'$	%unknown dyads	0.784	13	47.16	<0.001
PLC	# of dyads, displacements	0.800	12	23.50	<0.001

Six of the 15 matrices had a PLC below 0.05 and three others were below 0.10. Two other matrices had adjusted linearity values of 1.000 ( $h'$ ), but their PLC was still greater than 0.05 because lower probabilities are impossible in a group with only 5 individuals (Appleby, 1983). The combined PLC value was <0.001 in the meta-analysis using all of the matrices, and 0.009 when we used only the first matrix of each gorilla group. Ten of the 15 hierarchies have either an  $h'$  of  $\geq 0.80$  and/or a PLC of <0.05. All 5 of the remaining hierarchies have >30% of unknown dyads. Three of those hierarchies are the 1999-2001 data (which had low levels of observation) and the other two are early Group 5 years. Early results from some groups may be less reliable because females were not fully habituated, which may have biased observations towards particular individuals (e.g., Harcourt, 1979b; Watts, 1985). When the proportion of unknown dyads was less than 5%, the linearity indices were consistently higher than 0.95.

The  $R^2$  value from linear regressions indicated that the percentage of unknown dyads could explain more than 85% of the variance in the linearity indices ' $h$ ' & ' $K$ ', and more than 75% of the variance in  $h'$  (Table 2). The correlation between  $h$  and  $h'$  was highly significant (Pearson correlation:  $r = 0.989$ ,  $N = 15$ ,  $p < 0.001$ ), even though  $h'$  is specifically adjusted for unknown dyads, and such dyads varied from 0-65% of the total in each matrix. As expected, however, the adjustments did give  $h'$  a higher mean value than  $h$  (0.76 versus 0.69). About 80% of the variance in (log-transformed) PLC could be explained by the number of displacements observed in each matrix, and the total number of dyads (Table 2). The total number of dyads and the percentage of unknown dyads were significantly covariant (Pearson correlation:  $r = 0.565$ ,  $N = 15$ ,  $p = 0.028$ ). The PLC improves with more

**Table 3.** Distribution of interactions among dyads. Proportion of dyads with each number of interactions. Proportion of bidirectional dyads (with at least one displacement by each female).

#of interactions per dyad	%of all dyads	%bidirectional
0	34%	—
1	27%	—
2	16%	16%
3	10%	23%
4-5	9%	13%
6+	6%	3%

observed interactions, and worsens with more relationships to observe, suggesting that poorer values generally reflect an insufficient quantity of data, rather than actual nonlinearities in the dominance hierarchies. Nonetheless, some hierarchies may occasionally be nonlinear due to dominance transitions or lack of established relationships.

Overall, 34% of the dyads had no interactions, 27% had exactly one interaction, and 6% were bidirectional (with at least one displacement by each female, Table 3). Bidirectionality was not consistently higher in dyads with more interactions. Only 4% of all displacements were upward against the hierarchy, in which the subordinate displaced a higher ranked female (Table 2).

### *Potential factors affecting dominance*

#### Multiple regression summaries

There was a significant quadratic effect of age on rank, which accounted for almost 50% of the variance in the ranks (Table 4a,  $R^2 = 0.48$ ,  $F_{(2,46)} = 21.5$ ,  $p < 0.001$ ). Group tenure, natality, and maternal rank were not significant. Differences in age, age<sup>2</sup> and group tenure showed a significant relationship with the outcome of dominance dyads between two females (adjusted Tufto method, Table 4b). Forward and backward stepwise regressions yielded the same final logistic equation, which predicted the winner for 83% of the dyads ( $N = 156$ ). Although the logistic regression with group tenure had the greatest difference in log-likelihood (105.3), either mother's rank or natality was also significant when used instead (Table 4b-d). All three of those 'social

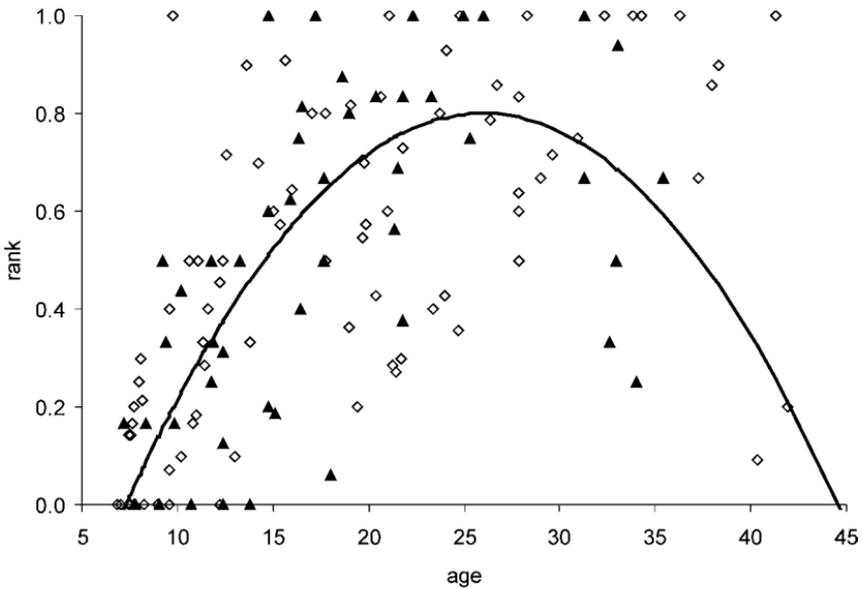
**Table 4.** Stepwise regressions for dominance relationships. (a) Linear regression for standardized dominance rank. (b-d) Logistic regressions for the winner of dominance dyads. (e) Pearson correlations coefficients for the independent variables in the logistic regressions, with Bonferroni adjusted probabilities for statistical significance: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ .

a	Estimate	S.E.	t-ratio	p-value
Constant	-0.750	0.221	-3.400	0.001
Age	0.119	0.024	5.050	0.000
Age2	-0.002	0.001	-4.173	0.000
b	Estimate	S.E.	t-ratio	p-value
Constant	0.087	0.238	0.364	0.716
Age	0.600	0.135	4.461	0.000
Age2	-0.012	0.003	-3.742	0.000
Tenure	0.253	0.065	3.890	0.000
2*[LL(N)-LL(0)] = 105.2952 with 3 df Chi-sq p-value = 0.0000				
c	Estimate	S.E.	t-ratio	p-value
Constant	0.088	0.233	0.376	0.707
Age	0.769	0.147	5.223	0.000
Age2	-0.014	0.003	-4.394	0.000
Nativity	2.510	0.634	3.961	0.000
2*[LL(N)-LL(0)] = 99.1030 with 3 df Chi-sq p-value = 0.0000				
d	Estimate	S.E.	t-ratio	p-value
Constant	0.019	0.218	0.085	0.932
Age	0.718	0.145	4.952	0.000
Age2	-0.013	0.003	-4.088	0.000
mom's rank	1.258	0.421	2.986	0.003
2*[LL(N)-LL(0)] = 86.1140 with 3 df Chi-sq p-value = 0.0000				
e	age	tenure	natality	
tenure	0.40**			
natality	-0.22	0.57**		
mom's rank	-0.37**	0.29**	0.58**	

variables' were significantly covariant with each other, and two of them were significantly covariant with age (Table 4e).

### Correlations with age

The regression results reflect an inverted u-shaped pattern between age and dominance, with low values for young females, peak values near age 25-30,



**Figure 1.** Standardized dominance rank versus age. Triangles are from the first matrix of each group; diamonds are from latter matrices of those same groups. The solid line is from a regression of rank versus age and age<sup>2</sup> using data from only the first matrices of each group.

and declining dominance thereafter (Figure 1). Individuals spanned a wide range of ranks. Of the 28 females who were evaluated more than once, 18 had at least one 'low' classification and one 'high' classification (Tables 5 & 6). Four of those 28 females were never observed to have a high ranking, but only one of them (Jen) was evaluated beyond age 12. Six were never observed to have a low ranking, but none of those females was evaluated below age 10.

The 15 matrices contain 12 evaluations of young adults (age <8), and all of them had a low ranking. There was only one instance where a young adult was ranked higher than a mature female. When a low-ranking female was evaluated in two successive matrices, she remained low-ranking in the latter evaluation only 17 of 35 times, which is not significantly different than the 50% probability that a randomly selected female will be low-ranking (Chi-square < 0.1, df = 1,  $p = 0.905$ ). When a high-ranking female was subsequently re-evaluated, she remained high-ranking in latter evaluation 40 of 45 times (Chi-square = 16.0, df = 1,  $p < 0.001$ ). Among the females with consistently high classifications, the most notable was 'Eff', who was top-ranked in almost every evaluation for 18-20 years. The only exception was

**Table 5.** Summary of dominance rankings for each female evaluated in more than one matrix.

Female	Number of matrices	Age range	Standardized dominance rank		
			Average	SD	Range
Aug	2	8-12	0.13	0.18	0.00-0.25
Bsh	2	8-17	0.48	0.47	0.14-0.81
Eff	7	22-41	0.99	0.04	0.90-1.00
Flo	4	25-42	0.45	0.35	0.09-0.75
Fud	4	15-34	0.86	0.19	0.60-1.00
Gin	3	9-21	0.47	0.12	0.33-0.56
Int	2	7-16	0.31	0.44	0.00-0.63
Jen	3	8-20	0.31	0.13	0.17-0.43
Kby	2	11-20	0.56	0.39	0.29-0.83
Kwr	5	9-25	0.38	0.42	0.00-1.00
Liz	6	23-28	0.65	0.15	0.50-0.83
Mag	4	8-22	0.35	0.40	0.00-0.71
Mah	2	8-17	0.61	0.56	0.21-1.00
Mar	2	31-37	0.67	0.00	0.67-0.67
Maw	3	8-20	0.25	0.29	0.00-0.57
Mur	2	7-8	0.15	0.21	0.00-0.30
Pan	6	16-35	0.45	0.23	0.20-0.79
Pap	5	9-38	0.66	0.39	0.00-1.00
Pet	2	13-15	0.75	0.35	0.50-1.00
Pic	4	10-15	0.46	0.26	0.10-0.70
Pop	2	8-10	0.30	0.14	0.20-0.40
Pty	7	8-27	0.60	0.32	0.00-0.86
Puc	7	11-33	0.80	0.19	0.50-1.00
Sha	3	9-21	0.26	0.25	0.00-0.50
Sim	6	11-25	0.40	0.14	0.20-0.55
Tuc	7	8-30	0.66	0.28	0.17-0.91
Umw	2	10-19	0.47	0.57	0.07-0.88
Wal	4	19-33	0.47	0.10	0.36-0.60

1988-89, when she was ranked second due to one observed displacement by Puc. According to qualitative observations by Fossey (1983), Eff was already top-ranked when Group 5 was habituated in 1967, so she may have been at or near the top for more than 25 years. Two of Eff's daughters (Tuc and Puc) had also been near the top for 15-20 years, even though Tuc transferred to Bm's group during that span. In Bm's group, Pap, Fud, & Tuc were repeatedly higher than Maw, Jen, Gin, & Sha for 11-13 years. Pap already had a high classification in Nk's group 7 years earlier, so she retained a high status for at least 18-20 years.

**Table 6.** Dominance ranks of each female in each matrix. Females above the dark line are considered 'high' ranking; those below are 'low' ranking. Females below age 8 are shown in italics. A hyphen before/after the initials indicates females who immigrated/emigrated; an asterisk indicates females who died.

Group	g4	g4	nk			bm	bm	bm		
Years	71-72	78	81-83			88-89	90-92	99-01		
1	Odg*	-Mac*	Pet-			Pap	Fud	Fud*		
2	Flo	Flo-	Pap			-Fud	Tuc	Pap		
3	<i>Pet-</i>	<i>Sim</i>	<i>Fud-</i>			<i>-Tuc</i>	<i>Pap</i>	Tuc		
4	Mai-	Aug	Pan-			Sha	Gin-	<i>Maw</i>		
5	Pap-	<i>Cle</i>	Sim-			Gin	Jen	Jen*		
6			Aug			Jen	Maw	Sha		
7						<i>Maw</i>	Sha	<i>Bka</i>		
								<i>Izz</i>		

Group	g5	g5	g5	g5	g5	g5	g5	sh	pb
Years	72-73	78-79	82-83	84-85	86-87	88-89	90-92	99-01	99-01
1	Eff	Eff	Eff	Eff	Eff	Puc	Eff*	Kwr	Mah
2	Liz	Liz-	Pty	Tuc	Tuc-	Eff	Puc	Kby	Puc
3	Mar	<i>Mar*</i>	Puc	Puc	Puc	Pty	Pty*	Pan*	Umw
4	<i>-Bry-</i>	Puc	Tuc	Pty	Pty	Pic	Pan	Wal	Bsh
5	Ida*	Pty	<i>Pop</i>	-Liz	Liz	Wal	Mag	-Kub	-Nze
6	<i>Pip-</i>	<i>Tuc</i>	<i>Mur</i>	-Sim	Sim	Liz	Kwr	Nah	Mag
7	<i>Pty</i>			Pop-	Pic	Pan	Pic-		Int
8				Mur-	-Wal	Sim	Liz*		-Gin
9				-Pan	Pan	Flo*	Wal		-Umu
10				-Pic	Kwr	Kwr	Sim*		-Nto
11				-Kwr	-Flo	Mag	-Kby		-Muk
12					<i>Mag</i>		Mah		-Umc
13							<i>-Bsh</i>		-Cyi
14							-Umw		-Mud
15							<i>Int</i>		Mak
16									-Gut
17									-Git

Of the four females who were ranked near the top for more than 15 years (Eff, Tuc, Puc, and Pap), none subsequently declined into a low ranking. Only three females had low rankings beyond age 30, and two were evaluated only once (Cyi & Ida), so it is unknown whether they ever held higher ranks. The other female, Flo, was ranked 2<sup>nd</sup> in a group containing 5 females at ages 24-31, and then ranked 9-11<sup>th</sup> in a group containing 11-12 females at

ages 39-42. Yet even her example is not compelling, because she changed groups during the intervening years; and even when she had held high ranks, the females below her had an average age of only 10.

### Social variables

In dyadic comparisons, the female with longer group tenure won 63% of decided dominance dyads, including 83% of dyads with younger females, but only 40% of dyads with older females. Females with a tenure advantage of at least 8 years were dominant in all 55 of the decided dominance dyads with younger females, and in 28 of 30 (93%) dyads with older females. Females in their natal group won 68% of decided dyads against nonnatal females, including all 34 dyads when they were older, but only 18 of 42 dyads (42%) when they were younger. Females whose mother was present were dominant in only 39% of decided dyads against females whose mother was absent, partly because they were younger than 85% of those other females. Females whose mother was present were dominant in only 30% of the dyads when they were younger than those other females, but they were dominant in 92% of dyads when they were older. The average standardized rank of the mother was 0.92, and even when she was top ranked, the daughter won only 49% of dyads against females whose mother was absent.

### Previous dominance status

The database contains 229 evaluations of female pairs that had already been evaluated in at least one earlier matrix. In 80% of those repeat evaluations, the female who had the higher ranking in the former evaluation was still higher ranking in the latter evaluation, which is significantly higher than a random 50:50 distribution (Goodness of fit Chi-square = 45.0,  $df = 1$ ,  $p < 0.001$ ). Excluding tied and unknown dyads, the winner in the former evaluation was also the winner in the latter evaluation 83% of the time ( $N = 144$  repeat evaluations, Goodness of fit Chi-square = 34.3,  $df = 1$ ,  $p < 0.001$ ). Thus, 80-83% of the repeat evaluations showed 'stability' in the dominance relationship of the female pair. About 80% of the repeat evaluations involved female pairs that were evaluated more than twice. The proportion of repeat evaluations that showed stability was not significantly correlated with the number of times that a female pair was evaluated (e.g. for  $N = 46$  rank switches, Kolmogorov-Smirnov test,  $D_{max} = 0.052$ ,  $p > 0.2$ ).

**Table 7.** Average changes for an 'established' female, who remained in the same group for two successive evaluations. Count of other females above/below the established female in the former/latter evaluations. Number of females who joined the latter hierarchy through maturation or immigration, and the number of females who left the former hierarchy through emigration or death. Number of rank switches with females above/below the established female.

	$N_a$ females above	$N_b$ females below	total	%below
<i>a) Counts of other females</i>				
former hierarchy	3.97	4.16	8.12	51%
latter hierarchy	3.57	5.76	9.33	62%
change	-0.40	1.60	1.21	
<i>b) Females leaving the former hierarchy</i>				
death	0.12	0.28	0.40	70%
emigration	0.41	0.45	0.86	52%
<i>c) Females entering the latter hierarchy</i>				
immigration	0.12	1.24	1.36	91%
maturation	0.02	1.09	1.10	98%
<i>d) Changes in group composition</i>				
total	0.67	3.05	3.72	82%
net	-0.40	1.60	1.21	
<i>e) Changes in dominance relationships</i>				
rank switches	0.57	0.57	1.14	50%

### *Potential pathways for rank changes*

When a female remained in the same group for two successive evaluations (an 'established' female), the average number of females above her ( $N_a$ ) dropped from 3.97 to 3.57 (Table 7a). An average of 0.12 females above her died, and another 0.41 females above her emigrated, while only 0.12 immigrants and 0.02 newly matured females entered the hierarchy above her (Table 7b-c). The ordinal rank ( $R$ ) equals  $N_a + 1$ , so the ordinal rank of the typical established female improved from an average of 4.97 to 4.57 in those successive evaluations (not shown). In those same evaluations, the proportion of females below her increased from 51% to 62% (Table 7a). This proportion equals her standardized rank, which therefore depends upon

changes that involve lower ranking females ( $N_b$ ). An average of 0.28 females below her died, and another 0.45 females below her emigrated, while 1.24 immigrants and 1.09 newly matured females entered the hierarchy below her (Table 7b-c). Through that influx of lower ranking females, total group size increased by an average of 1.21 females in the two successive evaluations (Table 7d).

When established females switch ranks, there is no net change in the average rank among those females, because one female gains rank, and the other female loses rank to the same extent. Therefore, the net changes in average rank arose from changes in group composition, not rank switches. Between the two evaluations, there were an average of 3.72 changes in group composition (maturation of new females, immigration, emigration, and deaths; Table 7b-d) and 1.14 rank switches among the established females (Table 7e). Therefore, most individual rank shifts occur through demographic changes in the group structure that favor established females, rather than from rank switches among those females.

In the 27 cases when females immigrated, their average rank in the next evaluation was 8.7 and their standardized rank was 0.38. On average, new immigrants were initially ranked above only 21% of the established females. In the 14 cases when females emigrated, their average rank in the preceding evaluation was 4.6 and their standardized rank was 0.44. Only 2 females have been evaluated shortly before and after a transfer: Sim's ordinal rank dropped from 5 to 6 in 1984, but her standardized rank increased from 0.2 to 0.5. Tuc's ordinal rank dropped from 2 to 3 in 1987, and her standardized rank dropped from 0.91 to 0.67.

During the fission of group 5 in 1993 (following the death of the dominant silverback), Eff moved to Pablo's group with four daughters and two granddaughters who were with her at the time (Robbins, 2001; Watts, 2001, 2003). Thus her matriline remained together. The only other matrilineal connections involved infant daughters who obviously stayed with their mothers (Wal and Pan). Both of the two new groups initially had six adult females, so the fission improved the average rank among those females from 6.5 to 3.5. Dominance relationships were not evaluated in the new groups until six years later, so it is unknown which particular females were the initial beneficiaries.

## Discussion

### *Strength and stability of dominance relationships*

Most, but not all of the matrices, resulted in hierarchies with a high adjusted Landau index and/or statistically significant linearity. When matrices in this study had less than 5% unknown dyads, linearity indices were consistently greater than 0.95. Among all the matrices, linearity measures were significantly correlated with the number of displacements observed, the number of dyads, and/or the proportion of unknown dyads. Therefore, poor linearity results for some matrices may reflect an insufficient quantity of data, rather than any actual circular relationships. Incomplete data may be due to both insufficient observation time, especially in groups containing many females, and a true lack of interactions among particular dyads. Variations in the quantity of data may explain why previous hierarchies based on displacements have not consistently shown significant linearity for this species (Harcourt, 1979a; Watts, 1985, 1994; Harcourt & Stewart, 1987, 1989; Stewart & Harcourt, 1987). Insufficient data may have also contributed to apparent non-linearities in a previous analysis of aggressive interactions, where 33% of dyads were tied or unknown (Watts, 1994). Although the linearity index ( $h'$ ) has been modified to adjust for dyads with no interactions, such unknown dyads have influenced linearity results in other studies too (Galimberti et al., 2003), and the degree of that influence may depend upon group size (Appleby, 1983; Koenig & Borries, in press). Therefore, linearity measures may be an unreliable indicator of the actual degree of linearity in the group if the number of unknown relationships is due to insufficient sampling effort.

While citing similar concerns about linearity measures, Isbell & Young (2002) proposed three other indicators of strong dominance relationships: a high rate of dominance interactions (cf. Sterck, 1999; Koenig, 2002), a low (<5%) frequency of upward interactions against the hierarchy, and high temporal stability. Female mountain gorillas reportedly have 'relatively high aggression rates' (1.1 per hour, Sterck & Steenbeek, 1997), but most of those interactions are undecided, and the rates of displacements are considered low in comparison with yellow baboons and vervet monkeys (Watts, 1985). Only 4% of the displacements were upward in this study, but Stahl & Kaumann (1999) report a value of 29% based upon the total number of agonistic interactions (citing Watts, 1994). Therefore, the validity of these interspecific

comparisons may depend on the relative importance of displacements, aggression, submissive behavior and/or other forms of agonistic interactions.

Temporal stability was greater than what would be expected by chance in this study, with over 80% of dyads maintaining the same dominant female when compared across successive evaluations. Most rank shifts occurred through changes in group composition, rather than switches in established relationships, and four females remained at or near the top of their groups for at least 15-25 years. Dominance relationships have shown stability for at least 10 years in studies of captive sooty mangabeys (Gust & Gordon, 1994; Stahl & Kaumanns, 1999), captive stump-tailed macaques (Rhine et al., 1989), and savannah baboons (Hausfater et al., 1982; Samuels et al., 1987; Combes & Altmann, 2001); but the dominance hierarchy was unstable for 75% of an 8.5 year study of captive patas monkeys (Goldman & Loy, 1997). Further study is needed to develop quantitative criteria for interspecific comparisons of such temporal stability.

When considering only the approach-retreat interactions (displacements), the linearity measures and the three indicators from Isbell & Young (2002) suggest an intermediate level of strength for the dominance relationships of female mountain gorillas. Hierarchies show linearity when matrices are full, but incomplete hierarchies partially reflect the low rate of displacements. The frequency of upward interactions is near the proposed 5% cutoff for strong versus weak relationships, and temporal stability is significant but not complete. However, these results for displacements should be viewed within a broader context of dominance behaviors. For example, female mountain gorillas lack formalized expressions of submission, such as the bared teeth displays of macaques, that are often associated with stronger dominance relationships (Hand, 1986; de Waal & Luttrell, 1989; Watts, 1994; Sterck & Steenbeek, 1997). In addition, Watts (1994) found that female mountain gorillas could not be placed in linear hierarchies when using all agonistic interactions: they exhibit high levels of bidirectionality in initiation of aggression, and the most common responses to aggression were to retaliate or ignore it. Submissive behavior, such as retreating during a displacement interaction, generally provides a clearer indication of dominance relationships than aggression (Rowell, 1966; Alados & Escos, 1992; de Vries, 1998). Submission can be considered a reflection of established relationships, whereas aggressive behavior may indicate a challenge to a dominance relationship (e.g.,

Walters, 1980). Nonetheless, when considering the results for aggressive behavior (Watts, 1994), and the lack of ritualized submission, the dominance relationships for mountain gorillas still seem weaker than when considering only displacements.

### *Dominance patterns and pathways*

Dominance rank of female mountain gorillas was strongly correlated with age, with only slightly lower rankings for the oldest females. Correlations between rank and age have been previously found for this species (Watts, 1985) and for captive lowland gorillas (Scott & Lockard, 1999), but those studies did not distinguish between the effects of age versus group tenure, nor did they show a decline at advanced ages. Female rank has also been observed to increase with age for chimpanzees (Wittig & Boesch, 2003) and several ungulates. These 'age-positive' trends are not necessarily related to body mass, and they continue beyond the age at which mass reaches a plateau (e.g., bison cows: Rutberg, 1983; red deer: Thouless & Guinness, 1986; mountain goats: Cote & Festa-Bianchet, 2001). Measurements of mass are not available for wild mountain gorillas, but life history theory proposes that the age of first parturition generally marks a transition when females divert their resource allocation from their own growth to reproduction. The age of first parturition is 8-12 years for mountain gorillas (Gerald, 1995), and females seem to reach their adult size by age 10-12 (pers. obs.). Female lowland gorillas reach their adult mass at age 10-14 in captivity (Leigh & Shea, 1996).

In some species, an individual who has won one contest has a higher chance of winning another, even with different individual (Fagen, 1977; Chase et al., 1994). Analytical models and computer simulations suggest that such cumulative 'winner effects' are needed to account for the degree of hierarchy linearity observed in nature, which cannot be entirely explained by individual traits such as body size (e.g., Beacham, 2003). Therefore, an older female may try to establish dominance while her younger competitors are still smaller, so she can maintain that dominance once the competitors reaches the same size. Our data suggests that dominance relationships can be maintained even after the subordinate reaches full adult size, but the rank switches show that such trends are not always permanent. Dominance instability is also reflected by the lower average ranks at advanced ages, although

the longitudinal analyses did not show compelling evidence of declines by specific individuals. This is due to only a few individuals being in the oldest age classes and therefore not being evaluated at more than one time interval. Lower average ranks have been observed for very old females of some species, but not others (see references in Coté, 2000).

Hypothetically, subordinates could circumvent any cumulative effects of previous interactions by transferring away from females with whom they have entrenched losing relationships. In addition to natal transfers by nulliparous females to avoid inbreeding, secondary transfers are also not unusual for mountain gorillas (Sicotte, 2001). However immigrants had lower ranks than emigrants in this study, and dominance was positively correlated with group tenure. Our results are consistent with qualitative observations by Fossey (1983), who suggested that females are ranked in the order that they join a group. Even when there is little resistance to immigration, resident females may make a special effort to establish higher rank over newcomers (Watts, 1991, 1994). Therefore winner effects are likely to be responsible for both tenure and age as being important variables in female dominance relationships.

Transferring females could choose a lone silverback or a small one-male group, where they would have few females above them, but offspring in those groups are more vulnerable to infanticide than in multimale groups (Watts, 1989, 2000). Female mountain gorillas transfer preferentially to multimale groups, so infanticide protection may be more important than group size and dominance rank in those decisions (van Schaik & van Hooff, 1996; Sterck et al., 1997; Watts, 2000). In contrast, females of western lowland gorillas appear to prefer smaller groups (Stokes et al., 2003), suggesting that feeding competition may have a stronger influence on their fitness and perhaps their dominance relationships than is the case for mountain gorillas.

Dominance based upon individual ability and experience, what we now refer to as individualistic hierarchies, is a contrast to social systems where dominance is based upon nepotism (e.g., baboons: Walters, 1980; Japanese macaques: Mori et al., 1989). Although in this study one matriline remained together during a group fission, we found little evidence of nepotism in the dominance rankings of female mountain gorillas, which is consistent with previous conclusions that there is little incentive for females to stay with close relatives (Harcourt, 1979a; Watts, 1985, 1994, 1997; Harcourt & Stewart, 1987, 1989; Stewart & Harcourt, 1987). Philopatry and mother's

rank may have helped to determine the winner of some dominance dyads, but it seems likely that group tenure is the more significant variable. Two females were briefly ranked adjacent to their top ranked mother, but one of those daughters subsequently emigrated, and four other daughters never had adjacent ranks. Daughters of other top-ranked females did not have high ranks. Even in species without nepotism, adjacent ranks may occasionally occur, especially if the daughters inherit traits that influence individual-based dominance (see references in Coté, 2000). Therefore, our few observations of adjacent ranks do not provide strong evidence for nepotism.

Although some female mountain gorillas maintained high ranks for at least 15-25 years, most females had both high and low ranks during their reproductive lifespan. Even if an age-based dominance system is entirely stable (no rank switches), each female can gradually rise through a wide range of the hierarchy upon the death of older, higher-ranked individuals. Any reproductive advantages she gains while dominant may be offset by the disadvantages from when she was subordinate (Gouzoules et al., 1982; Alados & Escos, 1992; Coté, 2000). In contrast, a female's rank in a nepotistic dominance system will generally be limited to the narrow range of her matriline, even if some rank switches occur within that matriline. Dominance can have greater impact on lifetime reproductive success when rank is consistent throughout adulthood (van Noordwijk & van Schaik, 1999). Therefore, even if a nepotistic hierarchy and an age-based hierarchy have comparable 'strength' by other measures (linearity, rate of expression, directionality, and stability) the nepotistic hierarchy will have greater impact on lifetime reproductive success. A weak relationship between rank and lifetime reproductive success would show that the ultimate benefits of dominance rank are limited and may help to explain why individualistic hierarchies are generally associated with weak dominance relationships.

Amongst species exhibiting individualistic hierarchies, 'age-positive' dominance hierarchies should be inherently more stable than the age-inverse hierarchies of mantled howlers (Zucker & Clarke, 1998) and hanuman langurs (Borries et al., 1991; Koenig, 2000). Rank switches should be common in an age-inverse system, as newcomers surpass the older females. In contrast, an age-positive hierarchy can have relatively few rank switches, and females who attain high rank may maintain such status for the rest of their lifetime. Temporal stability may provide a foundation for stronger dominance relationships, especially if weak or nonlinear hierarchies are most

common during dominance transitions (ibid). Thus, age-positive hierarchies may often have an intermediate strength, weaker than nepotistic but stronger than the age-inverse species (and of course stronger than species with no detectable hierarchies at all).

### *Female mountain gorillas and the socioecological model*

While outlining the socioecological model, Sterck et al. (1997) described three dimensions of dominance relationships: The structure of dominance hierarchies can be individualistic or nepotistic, and the strength of those relationships can vary from egalitarian to despotic. To simplify this discussion, we will disregard the third dimension (tolerance). Within-group contest competition (WGC) is expected to promote despotic dominance relationships, nepotism, and philopatry. In the absence of WGC, egalitarian relationships are predicted, coupled with dispersal in some species. Thus, Sterck et al. (1997) concluded that most primate females fall into three general classes: Resident-Nepotistic (RN), Resident-Egalitarian (RE), or Dispersal-Egalitarian (DE). Mountain gorillas have been classified as Dispersal-Egalitarian.

Van Schaik (1989) defined 'egalitarian' to include 'weakly linear' hierarchies, whereas Sterck et al. (1997) stated that they are fuzzy and non-linear, 'if they can be distinguished at all'. Mountain gorillas easily fit within van Schaik's definition, but Sterck's category seems narrower. From the latter perspective, it would be more precise to create a separate class for species with individualistic dominance structures, and to use the egalitarian category only for those with no discernable structure at all (e.g., muriquis: Strier, 1990; mountain baboons: Barrett et al., 1999). Thus, the most precise classification for female mountain gorillas would be 'Dispersal-Individualistic'.

Linear individualistic hierarchies are common in ungulates (e.g., Rutberg, 1983; Thouless & Guinness, 1986; Coté, 2000), and the present results fit within growing evidence for such dominance structures in primates. As Sterck et al. (1997) noted, callitrichids have individualistic and despotic dominance relationships, coupled with reproductive suppression and natal dispersal. Phayre's leaf monkeys also have linear hierarchies, which are probably individualistic because dispersal has been observed (Koenig et al., 2004). Individualistic hierarchies have been reported for captive sooty mangabeys (Gust & Gordon, 1994; Stahl & Kaumanns, 1999), but relationships may be nepotistic in the wild where dispersal has not been observed

(Range & Noe, 2002). Individualistic dominance rank affects the dispersal decisions of mantled howlers (Zucker & Clarke, 1998), and it has been correlated with reproductive success of chimpanzees and philopatric hanuman langurs (Borries et al., 1991; Pusey et al., 1997). Thus, linear individualistic hierarchies occur in a broad variety of primate species, spanning both the Resident and Dispersal categories. The level of competitive situations is more likely a determinant of dominance relationships than whether there is philopatry or dispersal. However, philopatry may allow for particular behavioral patterns, especially with kin and long-term associates, compared to species with dispersal.

Sterck et al., (1997) suggested that habitat disturbances may have caused some of the individualistic dominance structures in primates, such as howler monkeys and hanuman langurs (cf. Koenig, 2000). Mountain gorillas have suffered from habitat degradation, habitat loss, and poaching (e.g., Plumptre & Williamson, 2001), so some aspects of their social structure may reflect an evolutionary disequilibrium. Nonetheless, individualistic dominance structures could be evolutionarily stable when there is some competition for access to resources. Individualistic dominance hierarchies could involve some WGC for food, even in situations where females have an over-riding incentive to disperse (e.g., to avoid inbreeding) rather than remain with kin for coalitionary benefits. Individualistic dominance hierarchies may also form when females rely heavily upon a dominant male (e.g., for protection from infanticide and/or predation Watts, 2000). Such a scenario could promote within-group contest competition for proximity to the resident male, as well as dispersal to males who are better protectors. Finally, individualistic hierarchies could occur when species lack the cognitive abilities to form nepotistic coalitions, as Sterck et al., (1997) suggest for ungulates. Therefore, individualistic dominance structures may arise in either transitory or evolutionarily stable conditions.

Mountain gorillas feed on abundant, evenly-distributed herbaceous vegetation, so they appear to face little or no WGC (Watts, 1984, 1985). Some competition occurs over proximity to the dominant male, and females with infants have greater proximity than others (Harcourt, 1979c), but it is unknown whether dominant females spend more time near him than do subordinates. Aggression between females generally does not improve access to food or proximity to the dominant male (Watts, 1994). Thus it remains unclear why mountain gorillas risk injury through aggression (Watts, 2001),

and why they maintain a dominance structure. To help address these questions, further study is needed to examine the fitness consequences of dominance rank in this population.

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