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Fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*)

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Abstract The fitness consequences of dispersal decisions are difficult to quantify, especially for long-lived species with complex social systems. To calculate those consequences for male mountain gorillas, from the perspective of both subordinate and dominant males, we used behavioral and demographic data obtained over 30 years from the Virunga Volcano population to develop an agent-based model that simulates the life history events, social structure, and population dynamics of the species. The model included variables for birth rates, mortality rates, dispersal patterns, and reproductive skew. The model predicted an average lifetime reproductive success (LRS) of 3.2 for philopatric males (followers) and 1.6 for emigrants. The benefits of philopatry were most sensitive to opportunities for social queuing and to female transfer preferences, but philopatry remained the best strategy over a wide range of group conditions and hypothetical simulations. The average LRS for dominant males was 4.5 when a subordinate stayed and 4.6 when the subordinate emigrated. The dispersal decision of the subordinate male had little impact on the fitness of the dominant male because it came relatively late in the dominant male's reproductive life span, and it changed his group composition only incrementally. The fitness consequences for the dominant male were most sensitive to the degree of reproductive skew. Since subordinates suffer a fitness loss when they leave a group, they should accept whatever reproductive restraint is needed to avoid eviction, and the dominant male does not need to offer concessions for them to stay. The dominant male may offer reproductive concessions for other reasons, such as peace incentives or to confuse paternity, or he may not have complete control of reproduction within his group.

Keywords Dispersal · Mountain gorillas · Lifetime reproductive success · Reproductive skew · Agent-based model

Introduction

Dispersal patterns exhibited by group-living animals play an important role in determining their individual survival and reproductive success, as well as the population dynamics, genetic differentiation, and social system of their species (Greenwood 1980, 1983; Pusey and Packer 1987; Isbell and Van Vuren 1996; Kappeler and Van Schaik 2002). Dispersing individuals may emigrate voluntarily, or they may be forcibly evicted by more dominant individuals (Pusey and Packer 1987; Cant et al. 2001). Several potential costs and benefits of dispersal have been identified (for both the subordinate who decides whether to emigrate voluntarily, and dominant who decides whether to forcibly evict the subordinate), but quantification of those fitness consequences can be challenging (Lucas et al. 1997; Kokko and Ekman 2002). In primate species, evaluations have generally focused on whether subordinates should emigrate voluntarily (Alberts and Altmann 1995; Watts 2000; van Noordwijk and van Schaik 2001).

Subordinate individuals may emigrate voluntarily to obtain better access to mates, or to resources such as food, water, or shelter. According to the basic socioecological model for primates, the availability of food resources determines the distribution of females, which in turn influences the distribution of males (Sterck et al. 1997; Lindenfors et al. 2004). The opportunity for obtaining better resources must be weighed against the costs of finding those resources in an unfamiliar environment (Dobson et al. 1998). Animals may also disperse to avoid inbreeding in their natal group (Pusey and Wolf 1996; Perrin and Mazalov 2000), although they may lose breeding opportunities while solitary or in nonbreeding groups (Alberts and Altmann 1995). Dispersers forfeit alliances within the group they leave, and they may subsequently face greater aggression from other

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groups (Steenbeck et al. 2000; Korstjens and Schippers 2003). Increased mortality risks are a commonly cited cost of dispersal, particularly for species that are vulnerable to predation (Baker et al. 1993; Alberts and Altmann 1995).

Dominant individuals may evict a subordinate to reduce competition for resources or reproduction within a group (Crockett and Pope 1993), or they may tolerate a subordinate who assists them in such competition between groups (Byrne et al. 1987; Pope 1990; Packer et al. 1991). Dominant individuals may also keep a subordinate who enhances their own survival, or the survival of their offspring (Stacey and Koenig 1990; Solomon and French 1997). Subordinates may enhance the survival of offspring, even without providing direct parental care. For example, additional subordinates can improve vigilance against predators (Elgar 1989; Roberts 1996; van Schaik and Hoerstermann 1994), and they can enhance infanticide protection against extra-group males (Sekulic 1983; Pope 1990; Watts 2000; van Schaik and Janson 2000).

For both subordinate and dominant individuals, several game theory models have examined how dispersal decisions are influenced by the distribution of reproduction among the members of a group (“reproductive skew,” see reviews in Johnstone 2000; Hager 2003). In “transactional” models, the relationship between dispersal and skew depends upon the degree of relatedness between the dominant and subordinate individuals, the ecological constraints facing subordinates who disperse, and any improvement in group productivity when the subordinate stays. For example, the “concession” model assumes that dominants can completely control reproduction within a group, but not the composition of the group. It examines whether subordinates should emigrate voluntarily, based on the share of reproduction that the dominant “concedes” as an incentive for them to stay (Vehrencamp 1979, 1983; Stacey 1982; Reeve and Ratnieks 1993). In contrast, the “restraint” model assumes that dominants can control group membership, but not reproduction. It examines whether the dominant should forcibly evict subordinates, based on how much they restrain their reproduction in the group (Johnstone and Cant 1999).

The transactional models have been refined to examine many other factors, such as whether a subordinate should remain in a group while waiting to inherit the dominant position (“social queuing,” Kokko and Johnstone 1999; Ragsdale 1999). The “peace incentive” model examines whether the dominant male should offer concessions in order to avoid a potentially lethal fight with a subordinate (Reeves and Ratnieks 1993). The “tug-of-war” model assumes that the dominant male cannot completely control reproduction, and it examines how much effort each individual should devote to mating competition, while assuming that such competition reduces overall group productivity (Reeve et al. 1998). Aside from the game theory models, the “priority of access” model assumes that a dominant male cannot control reproduction with two fertile females simultaneously (Altmann 1962; Alberts et al. 2003).

Tests of the transactional models have often focused on the predicted relationships between reproductive skew

and relatedness (Jamieson 1997; Reeve 1998; Magrath and Heinsohn 2000). However, the models have become so numerous that almost any pattern of reproduction seems to be explained by one version or another (Cant and Reeve 2002). A second test of skew models has been to examine their assumptions, such as whether dominant individuals have full control over reproduction (Cant 1998, 2000; Clutton-Brock 1998a, 1998b; Reeve et al. 1998), and whether eviction is forced or voluntary (Cant et al. 2001), but criteria for assessing these variables are not easily determined for some species (Watts 2000). A third approach that we are using here is to examine the fitness consequences of dispersal, to determine whether concessions or restraint are necessary.

The primary goal of this paper is to evaluate the fitness consequences of dispersal decisions for male mountain gorillas (*Gorilla beringei beringei*). Part of our evaluation involves the relationships between dispersal and reproductive skew, so a secondary goal is to test existing theoretical models of those relationships. Mountain gorillas live in groups of 2 to 40+ individuals (average group size = 10), which typically contain several adult females and their immature offspring, and always at least 1 silverback (Stewart and Harcourt 1987; Kalpers et al. 2003). Both males and females may be philopatric or disperse (Harcourt et al. 1976). Although Watts (2000) suggests that moderate aggression from dominant males “may induce voluntary dispersal” from subordinates, there is no conclusive evidence that subordinates are forced to leave. Dispersing silverbacks become solitary males (lone silverback). Females transfer directly to a solitary male or to another group. Females may transfer multiple times in their lives; but they usually do not transfer with unweaned offspring, because unrelated males typically kill the infants (Watts 1989; but see Sicotte 2000).

Demographic transitions of social groups involve several pathways (Yamagiwa 1987; Robbins 1995, 2001; Yamagiwa and Kahekwa 2001). Group formation occurs either when females transfer to lone silverbacks or when groups fission. A group becomes multi-male (more than one silverback) when young males mature into silverbacks. Approximately 10–40% of groups have been multi-male over the previous three decades in the Virunga Volcano region (Kalpers et al. 2003). Multi-male groups can return to a one-male structure if an adult male emigrates or dies, or if the group fissions. When the silverback of a one-male group dies, the group disintegrates. If a breeding group loses all of its adult females, it becomes an all-male group. If a dominant male loses all of his group members, he becomes a lone silverback. Outsider silverbacks have not been observed to join or take over existing breeding groups.

The social system of mountain gorillas presents at least three benefits for a dominant male to tolerate a subordinate: higher probability of attracting females, earlier female fertility, and reduced risk of infanticide (Gerald 1995; Robbins 1995; Watts 2000). These benefits must be weighed against the potential costs of sharing reproduction with the subordinate, the risk of losing females if the group fissions, and the risk of losing his dominant status through usurpation (Robbins 2001, 2003). For a subordinate, the

benefits of philopatry include the potential opportunity for immediate reproduction. Collectively, subordinate males have performed up to 50% of observed matings in multi-male groups (Robbins 1999), and they have sired offspring in such groups (Bradley et al. 2001). Another benefit for followers (philopatric males) is the chance to attain a dominant role through usurpation, group fission, or death of the higher ranking males. These benefits must be weighed against the opportunities to form their own breeding group after emigration. Thus, the trade-offs for both males involve social queuing as well as reproductive skew (Kokko and Johnstone 1999; Ragsdale 1999; Hager 2003).

Direct measurements of these trade-offs have been limited due to the long life span of gorillas and the small number of habituated individuals and social groups (Robbins 1995; Watts 2000). Fortunately, however, substantial information has been collected about the factors that contribute to these trade-offs, which provide a strong foundation for quantitative models to calculate the fitness consequences of dispersal. A previous analytical model has suggested that followers have higher reproductive success than emigrants (Watts 2000), but it examined a limited range of social conditions, and did not calculate the fitness consequences for the dominant male. Here we use an agent-based model for a more comprehensive evaluation of the fitness consequences for both subordinate and dominant males. Agent-based models can provide greater flexibility than analytical formulations, allowing us to incorporate more detailed empirical data for a wider variety of factors, and to predict a wider variety of results from those factors (Lomnicki 1999; Diamond 2002; Pitt et al. 2003; Robbins and Robbins 2004).

In this paper, the base simulation of our agent-based model shows how the fitness consequences of an individual dispersal decision may depend upon characteristics of the specific situation, such as the number of adult males and females in the group, and the ages of the dominant and subordinate males, the rank of the subordinate, and the degree of reproductive skew. We also ran additional simulations to examine how those fitness consequences are influenced by key social factors such as female transfer preferences, the risk of infanticide, the age of first parturition for females, group fissions, usurpations of dominance ranking, and social queuing. We discuss these results within the context of reproductive skew models, to examine the relationships between reproductive share, dispersal decisions, and reproductive success.

Methods

Study area and population

The Virunga Volcano region contains three national parks straddling the borders of Rwanda, Uganda, and Democratic Republic of Congo with a combined area of 430 km². The national parks are surrounded by farmland, making the mountain gorillas an “island population” (Harcourt and Stewart 1981). Six censuses of the entire region have been

Table 1 Input parameters for the initial population

Parameter	Number	Age range (years)
Age classification		
Infants	33	0.0–3.5
Juveniles	27	3.5–6.0
Young adults	38	6.0–8.0
Blackbacks	16	8.0–12.0
Silverbacks	58	12+
Adult females	89	8+
Total	261	
Social structure		
Number of groups	31	
Mean group size	8	
Solitary males	8	
% Multi-male groups	42	
% Immature in groups	40	

conducted between 1971 and 2000, providing estimates of the population size, social structure, and age distribution (Kalpers et al. 2003). Groups are classified as one-male, multi-male, or all-male, based on their adult composition only; age classifications for the gorillas are defined in Table 1. The censuses have shown an average population growth rate of approximately 1% per annum, from 260 gorillas in 1971–1972, to almost 400 in 2000 (Kalpers et al. 2003).

Concurrently with these routine censuses, three to five groups of gorillas have been the focus of detailed studies at the Karisoke Research Center, which has provided precise information about birth rates, mortality rates, dispersal patterns, other life history events, and group structure (e.g., Gerald 1995; Robbins 1995, 2001; Sicotte 2001; 2000). Some demographic data have also been obtained from 12 groups that were habituated to the presence of tourists (Gerald 1995; Kalpers et al. 2003).

Overview of the agent-based model

Demographic data from the habituated groups were incorporated into an agent-based model that follows each individual over successive annual intervals, while also keeping track of groups and overall population structure (Robbins and Robbins 2004). The initial population in the model (Table 1) was based upon the results of the 1971–1972 census (Harcourt and Groom 1972; Groom 1973; Weber and Vedder 1983). To begin a simulation, the model selects the first gorilla from the initial population, adds a year to its age, and applies input probabilities for each life history event. The model compares the probabilities with output from a randomly generated number between 0 and 1. For example, if a female gorilla has a 5% probability of dying, then she survives only if the random number is more than 0.05. If she dies, the model reduces the total population size, and her group size, and the number of adult females. The model first evaluates death, then female transfers, births, male emigration, and changes in dominance ranking, using

a new random number for each life history event. After the model has considered all of the potential life history events for one gorilla, it repeats the process for each gorilla in the population. The gorillas are initially evaluated in a random order, but the same order is maintained in subsequent years.

Whenever the silverback dies in a one-male group, the model immediately processes the group disintegration. The remaining members are randomly assigned to another group or to a lone silverback. The new silverback evicts all males between the ages of 3 and 11, who are randomly assigned to an all-male group or to another lone silverback (Robbins 1995). The new silverback also kills all infants less than 3 years old (as reported for all 7–9 infants in 3–4 group disintegrations: Watts 1989). This infanticide is one of two types of deterministic death that the model treats separately from mortality probabilities. In addition, when infants are <2 years old, they automatically die if their mother dies (Robbins and Robbins 2004).

After reviewing all of the gorillas, the model next evaluates whether multi-male groups will fission (see below). It then advances 1 year, repeats the evaluations for each gorilla and each group, and continues for a total of 1,000 simulation-years. Each simulation involves 100 replicate “runs,” of these 1,000 simulation-years, to obtain more precise prediction values and a measure of variance. To avoid silverbacks with incomplete life histories, the model does not evaluate dispersal decisions during the first and last 35 years of each run. The computer model is written in Visual Basic and it operates within an Excel spreadsheet.

Parameters for the base simulation

The model uses separate mortality probabilities for each age and sex (Gerald 1995; Robbins and Robbins 2004; Table 2). Annual birth probabilities reflect that the age of first parturition is earlier for females in multi-male groups (9.9 years, vs 11.1 years in one-male groups); and that subsequent birth intervals are shorter when the previous offspring dies (2.0 years, vs 3.9 years when the previous child survives until the next one is born: Gerald 1995; Robbins and Robbins 2004; Table 3). The mortality and birth probabilities from Gerald (1995) combine to predict a 3% annual growth rate (Miller et al. 1998). To evaluate evolutionarily stable strategies with a stable population size (zero growth), the model continually adjusted birth probabilities for all females using the following equation:

$$P_A = P_1/[1 + (N/260)^6] \quad (1)$$

where P_A is the adjusted birth probability, P_1 is the input probability from Table 3, and N is the population size (Dobson and Lyles 1989). This density-dependent equation reduces the birth rate for larger populations, and increases the birth rate for smaller populations. The number 260

Table 2 Input parameters for individual gorillas: death probabilities

Input parameters: death probabilities		
Age	Males	Females
0	0.104	0.103
1	0.010	0.052
2	0.024	0.010
3	0.064	0.073
4–5	0.024	0.029
6–7	0.010	0.039
8–11	0.010	0.014
12–17	0.025	0.017
18–23	0.022	0.018
24–29	0.157	0.029
30–39	0.104	0.083
40	0.400	0.400
44	1.000	1.000

Table 3 Input parameters for individual gorillas: birth probabilities. *OMG* one-male group, *MMG* multimale group, *lived* previous offspring lived, *died* previous offspring died

Input parameters: birth probabilities					
Age	Age for first births		Interval for subsequent births		
	OMG%	MMG%	Years	Lived%	Died%
8	2	12	0	0	2
9	6	38	1	0	82
10	17	73	2	0	100
11	40	92	3	12	100
12	69	98	4	88	100
13	88	100	5	100	100
14	96	100	6	100	100
15	99	100	7	100	100
16	100	100	8	100	100

reflects the initial population size, and the exponent “6” fits within the range of 0.5 to 10 that Dobson and Lyles (1989) used in their hypothetical examples. Lower exponential values provide poorer population control, and higher values cause greater oscillations in birth rates, but such assumptions do not substantially affect the conclusions of this study. Due to the growth rate adjustments by Eq. 1, all simulated birth rates are lower than published values of 0.22–0.28 births/adult-female per year (Gerald 1995; Steklis and Gerald-Steklis 2001). Births in the research groups have not differed significantly from an equal sex ratio (Gerald 1995), so the model randomly assigns the sex of offspring with a 50% probability of either male or female.

The model gives females (age >6 years) a probability to transfer in each year that they are not nursing an infant below age 3. The model uses two different probabilities, depending upon whether the female is still in her natal group (Table 4). Whenever the probabilities indicate that a female will transfer, the model uses a weighting function to determine their type of destination. For example, the probability that a transferring female will choose a one-male

Table 4 Input parameters for individual gorillas: female transfers. Transferring females must be at least age 6, with no offspring below age 3. *OMG* One-male group, *MMG* multimale group. Annual transfer probabilities: natal transfer $P=0.300$, secondary transfer $P=0.062$

Input parameters: female transfers		
Transfer preferences	Transfer from	
Transfer to	OMG	MMG
Lone silverback	0.22	0.10
OMG	0.22	0.10
MMG	0.56	0.80

group is:

$$\frac{N_{\text{omg}} \times \text{FTW}_{\text{omg}}}{(N_{\text{omg}} \times \text{FTW}_{\text{omg}}) + (N_{\text{mmg}} \times \text{FTW}_{\text{mmg}}) + (N_{\text{lsb}} \times \text{FTW}_{\text{lsb}})} \quad (2)$$

where N_{lsb} , N_{mmg} , and N_{omg} are the number of lone silverbacks, multi-male groups, and one-male groups, respectively; and FTW_{lsb} , FTW_{mmg} , and FTW_{omg} are the weighting factors (transfer preferences) for female transfers to each potential destination (Table 4). The weighting function reflects two aspects of the empirical data: (1) females seem to prefer multi-male groups over other destinations (Watts 2000), and (2) females have limited opportunities to transfer, so their choices may be influenced by the relative availability of those destinations (Sicotte 2001). The weighting factors were empirically chosen so that the model would match the observed frequency that females transfer to each type of destination (Robbins and Robbins 2004). About 40–50% of females leaving a one-male group have gone to a multi-male group, compared with 60–90% of females leaving a multi-male group (Watts 2000).

Subordinate silverbacks in breeding groups are given a 50% emigration probability, at a randomly assigned “decision age,” between 12 and 18 years. Some silverbacks die or become dominant before reaching their decision age, so the 50% input probability leads to a 40% emigration frequency for males who reach age 12 within a breeding group. A 36% emigration rate (4 of 11 males) has been observed in the wild (Robbins 1995). When silverbacks are in all-male groups, the model gives them a 50% probability of emigrating each year, because nine emigrations occurred in 18 subordinate-years of observations of all-male groups (Robbins 1995).

When a subordinate remains in his breeding group at his decision age, he is classified as a “follower” and his dominant male is a “keeper.” When the subordinate leaves, he is classified as an “emigrant” and his dominant male is an “evictor.” These terms are not intended to indicate whether subordinates leave voluntarily or forcibly, but rather reflect the implicit assumption that dominance status implies more control over a subordinate individual than vice versa (an issue that we save for the Discussion). When a dominant male is involved with two or more subordinates, then one decision is randomly selected as the basis for his classification. The classification of dominant males is independent of

their classification as subordinates, and many males are not classified in either role (see Results). All classifications and analyses in this paper are limited to decisions in breeding groups.

Five group fissions have been reported during approximately 100 multi-male group years that habituated groups have been followed (Robbins 1995; Kalpers et al. 2003), so the model uses a 5% probability that a multi-male group will fission in a given year. The smallest multi-male group to fission had 11 members, but the model allows such fissions in groups with as few as 5 members in total. In addition, for purposes of computation expediency, fission automatically occurs in the very rare cases when a multi-male group has more than 90 members at the end of a year. During fissions, the model randomly gives the resulting new group between 10% and 50% of the members from the parent group, which reflects the observed range of such splits. At ages 0–4, gorillas stay with their mothers during fissions.

To assign dominance rankings, the model assumes that silverbacks mature into a peak “power,” which then gradually wanes (Fig. 1). Each year, a silverback’s probability of advancement in rank (usurpation) equals his power, minus the power of the next highest male. The shape of the power curve qualitatively resembles a trajectory proposed by Dunbar (1987), as well as a profile of dominance rankings in baboons (Alberts et al. 2003). The quantitative values were set so the usurpation algorithm in this model simulates the proportion of silverbacks at each age that have been dominant in the research groups (Robbins 1995; Williamson and Gerald-Steklis 2001). Silverbacks who are usurped (past-prime males) remain in the group and assume the former (lower) ranking of their usurper.

At the time of each birth, the model assigns paternity according to a geometric distribution (e.g., Nonacs 2000),

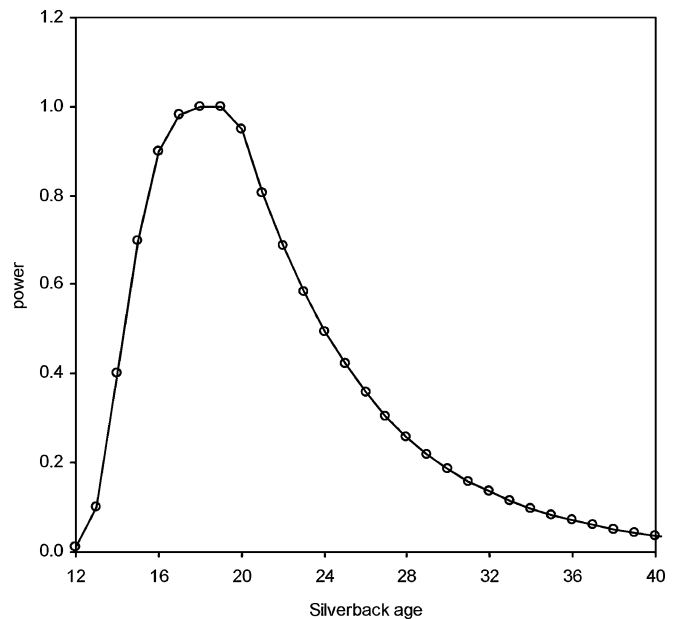


Fig. 1 Power factor for silverbacks versus age. See methods for explanation

where the relative probability of siring declines for silverbacks with a lower rank ($1, x, x^2, x^3 \dots$). We define a “skew factor” (SF) as $1-x$, so that when SF is high, a silverback’s chance of siring is very sensitive to his dominance ranking (high skew), and when SF is low a silverback’s chance of siring is insensitive to his dominance ranking (low skew). The skew factor has not yet been quantified for mountain gorillas, so each silverback is randomly assigned a value between 0 and 1. Although his individual skew factor remains constant throughout a silverback’s lifetime, his absolute probability of siring (P_i) will vary, depending upon the number of silverbacks in his group (N) and his dominance rank (R_i) at the time of each birth:

$$P_i = x_i^{(R_i-1)} / \sum_{j=1}^N X_j^{(R_j-1)} \quad (3)$$

Each year the model tallies the number of adult males and females that are with each silverback, and we report the average values from those tallies. For each silverback, the tally of adult males includes himself, so when he is solitary, he is counted as being with one adult male (and zero females). Throughout his lifetime, the model also tallies the number of births that occur in his groups (group births), and the number of his offspring. The reproductive share of each silverback equals his total offspring divided by his total group births. We define lifetime reproductive success (LRS) as the number of his offspring that survive to age 3. We partition the LRS into components of longevity, reproductive rate, and survival rate of offspring (Brown 1988). We define the fitness consequences of dispersal in terms of the reproductive advantages for the dominant and subordinate males that remain together. The “fitness gain for philopatry” by subordinate males equals the average LRS of followers minus emigrants. The “fitness gain for tolerance” by dominant males equals the average LRS of keepers minus evictors.

Parameter adjustments for additional simulations

We ran three simulations that alter the advantages of multi-male groups over one-male groups. Simulation 2 eliminates the female transfer preference for multi-male groups, by using the same weighting factor for all potential destinations. Simulation 3 eliminates all infanticide when the dominant male dies in a one-male group. Simulation 4 delays the age of first parturition for females in multi-male groups, giving them the same probabilities as females in one-male groups.

The other simulations examine conflicts within multi-male groups. Simulation 5 eliminates group fissions, except for the very rare cases when a multi-male group reaches 90 members. Simulation 6 eliminates usurpation, by giving all males the same power factor regardless of age. New silverbacks are assigned the lowest dominance ranking, and they advance only when higher ranking males leave the group through death, emigration, or fission. Simulation

7 eliminates social queuing, by eliminating usurpation and fission, and by having all subordinates emigrate to become solitary when the dominant male dies in a multi-male group. The group then disintegrates because it no longer has any silverbacks.

Results

Base simulation for subordinates

Only about half of all silverbacks experienced an emigration decision as a subordinate. Others are not classified as followers or emigrants, because they were in an all-male group (20%), or because they died (10%) or became dominant (20%) before their decision age. The LRS of followers is approximately double that of emigrants, representing a fitness gain for philopatry of 1.6 offspring (Table 5). This gain arises mainly because followers have a higher reproductive rate, but partly because their offspring have a higher rate of survival.

Social life history

As expected, followers spend more time as a pre-dominant subordinate, whereas emigrants spend more time solitary. Even though they do not emigrate, some followers still spend time as lone silverbacks, because their group ends through attrition. The average dominance tenure is higher for emigrants than for followers, but emigrants are dominant for about 2 years in all-male groups. More than 80% of both emigrants and followers become dominant, although 12% of the former are dominant only in an all-male group. The pathways to dominance are varied for both emigrants and followers, but most dominance tenures end through the death (Table 6). Followers spend more time as past-prime males, as their risk of usurpation is higher than for emigrants (Table 5). Followers spend about 75% of adulthood within multi-male groups, compared with only 25% for emigrants. For both emigrants and followers, about 60–70% of their multi-male group years occur while they are subordinates (when their group was obviously multi-male, since it included them as a subordinate).

Reproductive details

Followers and emigrants gain 70–80% of their reproductive success while dominant (Table 5). Almost half of the emigrants have no reproductive success, compared with only 22% of followers. Followers sire a smaller share of their group births, because they spend less time as dominants, and because their groups contain more adult male competitors. Nonetheless, their overall reproductive rate is more than double that of emigrants, because their groups also contain more females. Birth rates are essentially identical for females with followers versus emigrants.

Table 5 Average lifetime details for dominant and subordinate males in a dispersal decision

	Followers	Emigrants	Keepers	Evictors
LRS Partitions				
(L) Years as silverback	15.7	15.7	18.6	18.4
(R) Total offspring/year	0.29	0.16	0.33	0.36
(S) Offspring survival%	70	61	74	70
(LRS) Surviving offspring	3.2	1.6	4.5	4.6
LRS Standard deviation	3.5	2.5	3.9	4.1
Social life history				
Solitary years	0.2	4.7	0.7	0.7
Pre-dominant years	7.0	2.5	3.7	3.7
Dominant years	6.9	8.1	11.0	12.2
Dominant years in a breeding group	6.4	6.3	10.1	11.2
Past-prime years	1.6	0.4	3.2	1.8
Years in multimale groups	12.8	3.9	14.2	11.9
Age became dominant	18.4	17.8	16.3	16.2
% Became dominant	82	86	100	100
% Were dominant in breeding group	81	74	100	100
% Usurped	29	9	60	34
% Died in one-male group	30	84	18	43
Reproductive details				
RS while pre-dominant	0.9	0.3	0.5	0.5
RS while dominant	2.1	1.3	3.6	3.8
RS while past-prime	0.2	0.0	0.4	0.2
Average no. of males	3.1	1.5	2.6	2.3
Average no. of females	4.7	1.8	4.2	4.1
Births/female per year	0.16	0.16	0.16	0.16
Births/year in group	0.76	0.29	0.69	0.66
%Reproductive share	38	56	48	53
% With no reproductive success	22	45	9	10
Offspring survival details				
%Vulnerable/total offspring	18	21	14	15
%Infanticide/offspring	7	17	3	7
%Other deaths/offspring	23	22	23	23

Offspring survival

When followers and emigrants die, 18–21% of their offspring are younger than 3 years, and thus vulnerable to infanticide (Table 5). Only 30% of followers die in a one-male group, compared with 85% for emigrants. Therefore, infanticide losses are lower for offspring of followers: 7% versus 17% for offspring of emigrants. Other mortality probabilities are identical for offspring of followers and emigrants, so offspring of followers have higher overall survival.

Impact of conditions at the time of the dispersal decision

The LRS of emigrants is almost entirely independent of the characteristics of the group they left behind (results not shown). In contrast, the LRS of followers will depend upon the group in which they remain. Therefore, the fitness gains for philopatry depend upon the conditions at the time of the dispersal decision. The fitness gain is greater for followers in groups with more mating opportunities (females) and less male competition (Fig. 2a). Philopatry is

more rewarding for subordinates with an aging dominant male, who is more vulnerable to both death and usurpation (Fig. 2b). The benefits of philopatry are also greater for higher ranking subordinates, and for those who can gain more reproduction while subordinate (low skew in Fig. 2c). Philopatry remained the better strategy over the full range of all conditions shown in Fig. 2, even when subordinates gain little or no reproduction (high skew in Fig. 2c).

Base simulation for dominant males

About 20% of silverbacks never become dominant at all, 25% are never dominant in a breeding group, and 65% never face an eviction decision while dominant in a breeding group. Of the dominant males who have such eviction decisions, about 50% face only one decision; 25% face two; 12% face three, and 12% face four or more decisions (Table 7). LRS is higher for dominants with more eviction decisions, because they also have longer dominance tenures in groups with more females. For dominant males with a given number of decisions, however, the outcome of those decisions had diverging impacts on LRS (Fig. 3).

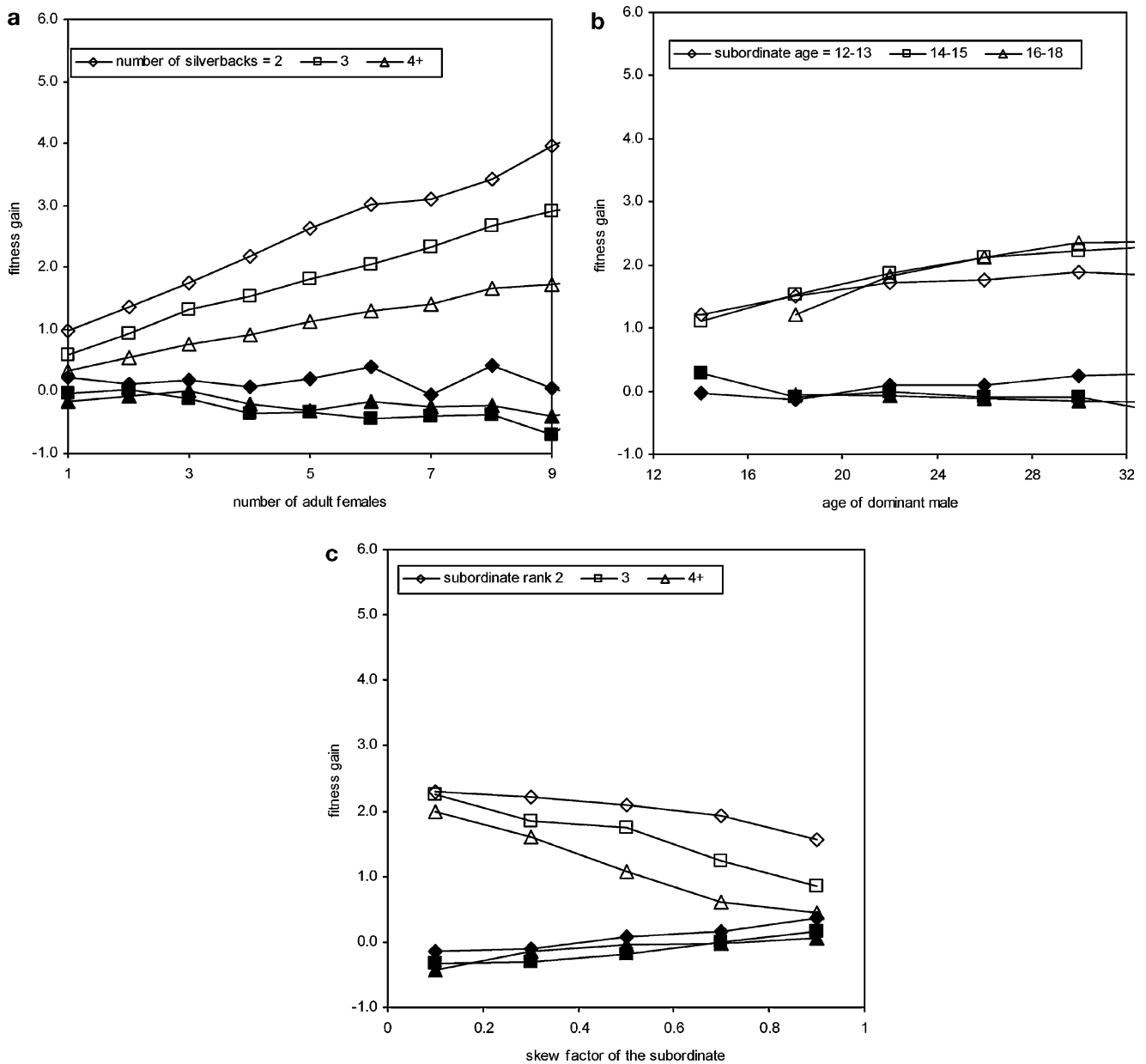


Fig. 2a-c Direct fitness gains when a subordinate stays, versus group/social characteristics at the time of the decision. **a** Number of adult males and females in the group, **b** age of the dominant and subordinate males (each result is lumped from ± 2 years of age for

the dominant male), and **c** dominance rank and skew factor for the subordinate (each result is lumped from $\pm 10\%$ skew). *Open symbols* are fitness gains for the subordinate male; *closed symbols* are for the dominant male

For dominant males involved in only one decision, the net fitness gains were 0.3 when the subordinate stayed. When dominants faced two decisions, they had a very slight fitness gain by keeping one subordinate, and a fitness loss by keeping both. If dominants had more than two decisions, their average LRS dropped with each subordinate they kept. When those divergent trends are combined, the average LRS is virtually identical for keepers versus evictors, representing no overall fitness consequences for the reproductive strategy of tolerance (Table 5). Evictors have a higher reproductive rate, but offspring of keepers have higher survival.

Social life history

The risk of usurpation is about double for keepers versus evictors, so dominance tenures are about 10% longer for evictors, and keepers spend more time as past-prime males. Keepers spend about 75% of adulthood within multi-male groups, compared with 65% for evictors. Evictors still spend most of their reproductive life span in a multi-male group, because 60% of that time occurs before the eviction decision, and even when one subordinate leaves, the evictor may still have other silverbacks in the group.

Table 6 Pathways to begin and end a dominance tenure. Followers typically become dominant through the pathways within a group, and emigrants typically become dominant through pathways for lone silverbacks. These results also include silverbacks who were not counted as either followers or emigrants, because they were in all-male groups or they became dominant before their decision age. The results do not include silverbacks who died before becoming dominant. *LSB* lone silverback

% Of total	% Of subtotal	Pathways
Pathways to become dominant from within a group		
18	38	Death of the dominant male
19	41	Usurp the dominant male
10	21	Group fission
	100	Subtotal for within a group
Pathways for LSB to become dominant		
24	46	Female transfer to LSB
17	33	LSB accepts evictees to form an all-male group
11	21	LSB adopts an orphan group
	100	Subtotal for lone silverbacks
100		Total for all silverbacks who become dominant
Pathways to end a dominance tenure		
64		Death while dominant
19		Usurped by a subordinate
17		Group attrition (only leader left)
100		Total for all silverbacks who become dominant

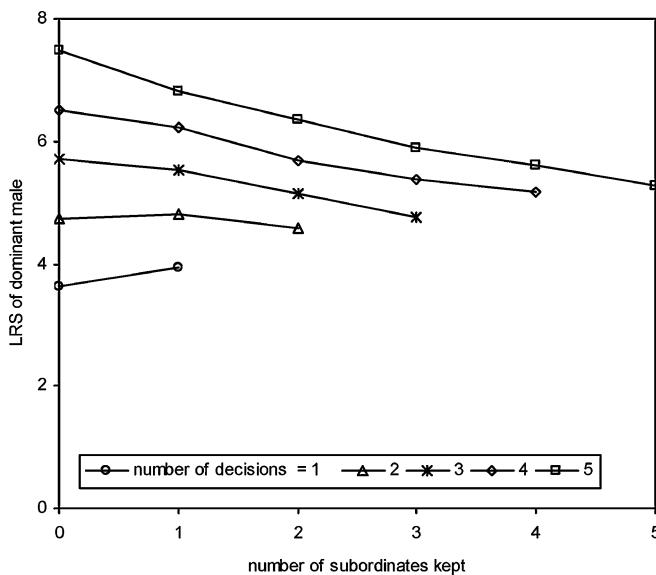


Fig. 3 Lifetime reproductive success (*LRS*) for the dominant male, versus his number of eviction decisions, and the number of subordinates he retained

Reproductive details

Keepers and evictors both have about 80% of their reproductive success while dominant (Table 5). Keepers sire a smaller share of their group's births, again because they spend less time as dominants, and because their groups contain about 10% more adult male competitors. The

keeper and follower typically stay together for an additional 5 years, until the follower leaves the group through fission, or either silverback dies. The average number of females in a group is only 3% higher for keepers than for evictors, a difference of 2.5 female-years. Birth rates are essentially identical for females with both types of silverbacks.

Offspring survival

When keepers and evictors die, 14–15% of their offspring are younger than 3 years, and thus vulnerable to infanticide (Table 5). About 40% of evictors die in a one-male group, compared with only 20% for keepers. Therefore, infanticide losses are lower for offspring of keepers: 3% versus 7% for offspring of evictors.

Impact of conditions at the time of the decision

Dominant males obtain a slight fitness gain by keeping one subordinate, and a slight fitness loss by keeping additional subordinates (Fig. 2a). Similarly, fitness consequences are slightly worse for dominants who keep lower ranked silverbacks, because those low rankings can only occur in groups with additional subordinates (Fig. 2c). The *LRS* of a dominant is higher in groups with more adult females (Table 7), but that trend occurs regardless of whether a subordinate stays or leaves (results not shown). Therefore, the number of females has little impact on the net fitness consequences of the eviction decision (Fig. 2a). The net fitness consequences for the dominant male are also fairly insensitive to his age, and to the age of the subordinate at the time of the decision (Fig. 2b). Keeping is a better strategy for dominant males when skew is high (Fig. 2c), and skew has more impact than any other factor in the simulations. Overall, however, the fitness consequences remain small for dominant males over the full range of conditions shown.

Additional simulations

Benefits of multi-male groups

In the absence of female transfer preferences (simulation 2), the fitness gains for philopatry were less than half of the base simulation (Table 8). This predicted shift reflects an average loss of 0.6 surviving offspring for followers who acquire fewer females, and an average gain of 0.6 surviving offspring for emigrants who acquire more females (Table 8). Yet even with the equal female transfer preferences, followers still had more females than emigrants (an average of 3.3 vs 1.9 throughout their respective lifetimes) because followers inherit groups that already have females, whereas emigrants are more likely to acquire their females incrementally. Female transfer preferences have little impact on the fitness gains for tolerance by dominant males because the overall female transfer rates are low.

Table 7 Social life history for silverbacks with each number of eviction decisions while dominant. *LRS* lifetime reproductive success

No. of eviction decisions	% Of all Silverbacks	Average age at death	Dominant years	Average no. females	Infanticide losses as % of offspring	LRS
0	64.6	27.3	8.8	2.0	13.2	1.7
1	18.3	30.1	11.5	3.5	5.7	3.8
2	8.8	30.6	11.5	4.4	3.1	4.8
3	4.3	31.1	11.6	5.2	2.0	5.5
4	2.1	31.3	11.6	5.9	1.2	5.9
5	1.0	31.5	11.7	6.5	0.9	6.4
6	0.5	31.9	11.9	7.0	0.7	6.6
7	0.2	32.1	11.9	7.4	0.5	6.7
8	0.1	31.8	12.0	8.1	0.4	7.3
9	0.1	32.7	12.9	8.4	0.4	7.3

Table 8 Simulations for each of the factors that influence the fitness consequences of dispersal decisions. *LRS* (lifetime reproductive success) of the subordinate and dominant males, and the fitness gains when they stay together

Simulation		LRS	LRS	Fitness gain for:	LRS	LRS	Fitness gain for:
	Adjustments to the base simulation	Followers	Emigrants	Philopatry	Keepers	Evictors	Tolerance
1	Base simulation (no adjustments)	3.2	1.6	1.6	4.5	4.6	-0.1
Benefits of multimale groups							
2	No female transfer preference	2.6	2.0	0.6	4.1	4.2	-0.1
3	No infanticide	3.1	1.7	1.4	4.2	4.4	-0.2
4	Same age for first parturition	3.1	1.6	1.5	4.4	4.5	-0.1
Conflicts within multimale groups							
5	No fission	3.3	1.4	1.9	4.6	4.7	-0.1
6	No usurpation	3.1	1.7	1.4	5.3	5.0	0.2
7	No queuing	2.0	2.6	-0.6	5.9	6.0	-0.1

The fitness gains for philopatry also reduced in the absence of infanticide (simulation 3; Table 8). Emigrants are more likely than followers to die in a one-male group, so their offspring would be more likely to benefit from the elimination of infanticide. In the absence of infanticide, dominant males would have greater incentive to evict subordinates, but the fitness gains for tolerance would only drop from -0.1 to -0.2 surviving offspring. The female age of first parturition had little impact on the fitness consequences of emigration decisions by subordinates and the eviction decisions by dominant males (simulation 4).

Conflicts within multi-male groups

The best case for philopatry occurred in the absence of group fissions (simulation 5). For a follower, the risk of losing potential mates through fission is greater than the rewards of becoming dominant through this pathway. Fission reduces the number of potential mates for dominant males, so without this risk, LRS increases for both keepers and evictors, but the net difference between the two strategies remains small (Table 8). The best case for tolerance occurred in the absence of usurpation (simulation 6), which correspondingly reduced the incentive for philopatry.

When we eliminated social queuing, simulation 7 provided the only example of net fitness losses through philopatry (Table 8). In that case, followers essentially became “delayed emigrants,” since they had no opportunity to inherit their natal group, and they left when the dominant male died. Lack of social queuing had little impact on the direct fitness of dominant males, because the lack of usurpation and fission were offset by a higher risk of infanticide.

Discussion

Costs and benefits of philopatry by subordinates

The model predicts that most subordinates should try to stay in their group, where their average LRS is approximately twice that of emigrants. This prediction is consistent with previous calculations by Watts (2000), who concluded that the two most important advantages for followers are a higher probability of becoming dominant in a breeding group, and access to more females throughout their reproductive lifetime. Our analysis confirms those advantages for followers, and also predicts that their offspring are less likely to die from infanticide. However, Watts (2000) did

not show how the fitness consequences vary over the full range of group conditions (e.g., his followers always had at least four adult females), and he suggested that wider variations in such conditions could explain why some silverbacks emigrate and others do not. In contrast, our analysis shows that philopatry remains the better strategy over a wide range of conditions (number of males and females in the group, ages of the subordinate and dominant males, subordinate rank, and reproductive skew).

Followers have higher fitness due to the benefits of social queuing, and their worst scenario arose when we eliminated queuing in simulation 7. Our model's predictions are consistent with reproductive skew models of social queuing, which show that even complete skew can be acceptable to subordinates, if they can subsequently inherit a dominant role in the group (Kokko and Johnstone 1999; Ragsdale 1999). Philopatry is essential for social queuing with gorillas, because unlike other species (e.g., baboons: Alberts and Altmann 1995, howler monkeys: Pope 2000; Hanuman langurs: Borries, 2000), dispersing adult males do not immigrate into established groups. In addition to forfeiting their queuing opportunities, emigrants also lose mating opportunities while solitary, and they continue to have lower mating opportunities while they acquire females incrementally (unless they acquire the remnants of a disintegrated group). This incremental approach contrasts with some models of territorial species, which have equated LRS with the probability of simply acquiring a territory (e.g., birds: Kokko and Eckman 2002).

The fitness of emigrants is further limited by unfavorable transfer preferences from females to lone silverbacks, and by low overall rates of such female transfers. Our first two simulations illustrate that male dispersal strategy is sensitive to female transfer decisions. These results are consistent with the "socioecological model," which predicts that male reproductive strategies are based upon the spatiotemporal distribution of females (Sterck et al. 1997; Lindenfors et al. 2004). When feeding competition is low, as currently observed in the Virunga Volcano region due to the abundance of evenly distributed food resources, females may prefer the extra protection that multi-male groups offer against infanticide (Watts 1996). In this scenario, the base simulation predicted that philopatry is the better strategy for males. In the absence of such female transfer preferences (simulation 2), philopatry became less favorable, although some advantage remained because followers still had access to more females. Simulation 2 may be more representative of western lowland gorillas (*G. gorilla*), where food resources are more dispersed in time and space, and females preferentially transfer to smaller groups (Parnell 2002; Stokes et al. 2003; Robbins et al. 2004). In contrast with the variable dispersal patterns of male mountain gorillas, male emigration is virtually universal for lowland gorillas.

It is likely that gorillas initially evolved under ecological conditions that favor a predominantly one-male mating system because they do not exhibit other traits that are characteristic of multi-male systems, such as large testes size, long estrous periods, and large female sexual swellings

(Harcourt 1995; Nunn et al. 2001; Robbins 2003). Therefore, living in the Virunga Volcanoes may represent a recent expansion of gorillas and they still may be adapting to the ecological conditions of the highland environment. While female dispersal strategies may be well adapted to this environment (Watts, 1996), the current patterns of male dispersal could reflect an evolutionary disequilibrium, with some male mountain gorillas emigrating voluntarily even though the current fitness consequences are unfavorable. A phylogenetic analysis of the socioecological model has shown an evolutionary lag in the way that males respond to the distribution of females (Lindenfors et al. 2004). Such an evolutionary lag could be especially long with gorillas, due to the complexities of social queuing. Emigration is a once-in-a-lifetime decision for a silverback, and the consequences of that decision unfold throughout his entire lifetime (and beyond, through infanticide risks to his offspring). Many emigrants fare just as well as many followers, with considerable variance for both strategies. If a silverback cannot reliably assess the optimal strategy, then adaptations within each individual lifetime may be limited, and social queuing may evolve more slowly than other behaviors. Additional study is needed to more fully explore the inter-relationships between male and female dispersal patterns, with particular emphasis on differences between lowland and mountain gorillas.

Even if philopatry is the evolutionarily stable strategy for most silverbacks, some voluntary emigration could still occur when subordinates find an unusually promising opportunity (such as an outside group with an aging dominant male and many females). However, observations have not shown immediate opportunities for emigrants, and only 20% of them have been reported to achieve any reproductive success at all (Robbins 1995). Other subordinate males could emigrate voluntarily to avoid inbreeding, which has been cited as the major reason for natal dispersal of female mountain gorillas (Sicotte 2001). However, with known patterns of female dispersal, our model predicts that females spend less than 10% of their reproductive years in their natal group. Therefore, most subordinate males should have unrelated breeding partners even without emigrating. Inbreeding avoidance could be a factor in some instances of silverback dispersal, but it probably would not be a decisive factor in most cases.

Costs and benefits of tolerance by the dominant male

Eviction decisions had small fitness consequences for dominant males over a wide range of group conditions, because the impact of the typical decision came relatively late in their career; and it had only an incremental impact on their social setting and status; and it had offsetting costs and benefits. The consequences of eviction decisions were most sensitive to the potential costs of usurpation and the potential benefits of infanticide protection (simulations 3 and 7), factors that arise in the final years of life. Empirical data are consistent with the model in showing that emigration/expulsion decisions tend to occur in groups with more

silverbacks (Robbins 1995), so any one decision has only limited impact on whether a silverback has a one-male or a multi-male group.

The model predicts that dominant males obtain a slight fitness gain by keeping one subordinate, and a slight fitness loss by keeping additional subordinates (Fig. 2a). Those predictions reflect the previously reported reproductive advantages for multi-male groups over one-male groups (Robbins 1995, 2001; Watts 2000), but those studies do not make further distinctions between multi-male groups with different numbers of silverbacks. Since such distinctions were unavailable for the input parameters of the model, our predictions about the additional subordinates should be viewed with caution. The additional subordinates may represent “backup insurance” to maintain a multi-male group structure if another silverback dies or emigrates, but meanwhile they still can compete for reproductive share, and they ultimately may pose a usurpation risk for the dominant male.

The model may underestimate the incentive for dominant males to tolerate a subordinate, because it does not account for the inclusive fitness that they gain by improving the reproductive success of a related subordinate (Hamilton 1964). If the success of a follower comes at the expense of other (closer) relatives, however, the net inclusive fitness benefits for the dominant male could be small or even negative. Additional study is needed to quantify the impact of inclusive fitness, which becomes increasingly complex when more than two individuals are involved (Johnstone et al. 1999). Inclusive fitness could also explain why some dominants allow a subordinate to stay, while no dominants have been observed to accept an outsider silverback (especially if silverbacks use social familiarity as a proxy for kin recognition: Harcourt 1979, Harcourt and Stewart 1981).

Implications for reproductive skew

Genetic analysis has shown that subordinates sire offspring in multi-male groups of mountain gorillas (Bradley et al. 2001). According to our model subordinates suffer a fitness loss when they leave a group, regardless of the level of reproductive skew, so the dominant male does not need to offer reproductive concessions for them to stay (Vehrencamp 1979, 1983; Stacey 1982). Instead, the dominant male may offer concessions, such as a peace incentive (Reeve and Ratnieks 1993), to avoid a potentially lethal fight with subordinates. Mating competition has been known to cause lethal injuries among silverbacks, and the high costs of fighting have been cited as a reason for low skew with lions (Packer et al. 2001), Galapagos hawks (Faaborg et al. 1995), and the pukeko (Jamieson 1997). It is unclear, however, how researchers would quantify this key parameter in the peace incentives model. The dominant male may also offer concessions so that subordinates will have a greater incentive to help protect the offspring from outside males, and so the subordinates will not commit infanticide if the dominant male dies. For that strategy, the dominant male must weigh the potential benefits of higher

infant survival against the potential risk that he will lose paternity to the subordinate (Kappeler and van Schaik 2004).

If the dominant male does not offer reproductive concessions for any reason, the observed siring by subordinates is evidence that he cannot completely control reproduction in the group. Incomplete control by the dominant male has been cited as a reason for subordinate siring in rhesus monkeys (Widdig et al. 2004), hyenas (Engh et al. 2002), meerkats (Clutton-Brock et al. 2001), and acorn woodpeckers (Haydock and Koenig 2003). Further study is needed to test incomplete control models with silverback gorillas. For example, a key assumption in the tug-of-war model is that mating competition reduces group productivity (Reeve et al. 1998; Langer et al. 2004). Male mating competition has been observed to reduce female reproduction in Hanuman langurs (Srivastava and Dunbar 1996) and colobus monkeys (Dunbar 1987), reportedly due to increased stress, but such effects have not been examined with gorillas. The priority of access model probably does not explain most cases of subordinate siring with this species because the probability of co-cycling is low for female mountain gorillas (Dunbar 2000; but see Alberts et al. 2003 for baboons and for references about other species). Nonetheless, the relevance of that model could be further quantified by examining whether subordinate siring coincides with such co-cycling.

When a dominant male cannot completely control reproduction, some subordinates may need to restrain their reproduction to avoid eviction (Johnstone and Cant 1999). Our model indicates that subordinate silverbacks should practice whatever restraint is required, rather than risk eviction, because even with no subordinate siring, they can still gain from philopatry through the ultimate benefits of social queuing (Fig. 2c). The required level of restraint corresponds to the level of skew where the fitness consequences of tolerance are zero for the dominant male (Johnstone and Cant 1999). Our model predicts that such a threshold occurs at an intermediate skew factor (Fig. 2c), so the reproductive share of subordinate silverbacks could determine whether the dominant male should evict them. Thus our results are consistent with incomplete control theory, within the limits defined by restraint models, as influenced by the costs and benefits of social queuing.

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