RESEARCH ARTICLE

Simulation of the Population Dynamics and Social Structure of the Virunga Mountain Gorillas

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An agent-based model was developed to simulate the growth rate, age structure, and social system of the endangered mountain gorillas (*Gorilla beringei beringei*) in the Virunga Volcanoes region. The model was used to compare two types of data: 1) estimates of the overall population size, age structure, and social structure, as measured by six censuses of the entire region that were conducted in 1971–2000; and 2) information about birth rates, mortality rates, dispersal patterns, and other life history events, as measured from three to five habituated research groups since 1967. On the basis of the research-group data, the ''base simulation'' predicted a higher growth rate than that observed from the census data (3% vs. 1%). This was as expected, because the research groups have indeed grown faster than the overall population. Additional simulations suggested that the research groups primarily have a lower mortality rate, rather than higher birth rates, compared to the overall population. Predictions from the base simulation generally fell within the range of census values for the average group size, the percentage of multimale groups, and the distribution of females among groups. However, other discrepancies predicted from the research-group data were a higher percentage of adult males than observed, an overestimation of the number of multimale groups with more than two silverbacks, and an overestimated number of groups with only two or three members. Possible causes for such discrepancies include inaccuracies in the census techniques used, and/or limitations with the long-term demographic data set obtained from only a few research groups of a long-lived species. In particular, estimates of mortality and male dispersal obtained from the research groups may not be representative of the entire population. Our final simulation addressed these discrepancies, and provided a better basis for further studies on the complex relationships among individual life history events, group composition, population age structure, and growth rate patterns. Am. J. Primatol. 63:201–223, 2004. © 2004 Wiley-Liss, Inc.

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INTRODUCTION

An understanding of population dynamics is important to behavioral ecologists and conservation biologists alike, but rarely can an entire population be intensively monitored over a long period of time. Additionally, for species that live in social groups, it is important to monitor not only patterns of population growth or decline, but also other variables, including group size, age/sex structure of social groups, and dispersal patterns. To obtain information on population dynamics and social structure, one can perform periodic censuses for a large proportion of the population, or conduct more continuous research on a selected subpopulation or social groups. When both methods are used for the same population, one can compare the results to reconcile the strengths and pitfalls of each method, and to develop a more consistent interpretation of all the data collectively [e.g., Haydon et al., 1999]. The main purpose of this paper is to compare estimates of population dynamics obtained from routine censuses with long-term demographic data from research groups of the critically endangered mountain gorillas (*Gorilla beringei beringei*) of the Virunga Volcanoes region of Rwanda, Uganda, and the Democratic Republic of Congo.

Six censuses of the entire Virunga Volcanoes region (430 km^2) were conducted between 1971 and 2000, providing estimations of the overall population size, age structure, and distribution of the gorillas into social groups [Aveling & Harcourt, 1984; Groom, 1973; Harcourt & Groom, 1972; Kalpers et al., 2003; Sholley, 1991; Vedder & Aveling, 1986; Weber & Vedder, 1983]. Unfortunately, human disturbances have been a major factor in the area [Kalpers et al., 2003; Plumptre & Williamson, 2001; Stewart et al., 2001; Weber & Vedder, 1983]. In the late 1960s, approximately 125 km^2 of the Rwandan park was converted into farmland. Such habitat loss was stopped in the 1970s, but the gorillas continued suffering from habitat degradation and poaching, and the population declined by about 0.8% per year. The 1980s were characterized by improved conservation activities, such as removing snares, patrolling for poachers, and educating the surrounding populace. The gorilla population responded with approximately 3.0% growth per year. Through the 1990s, the region was marred by the civil unrest, and at least 4–5% of the gorillas died as a direct result of military activity. Despite these pressures, however, the population increased by about 1.0% per annum.

Although it is believed that the census techniques used accounted for 90–95% of the entire population, some potential limitations have been reported. For such censuses, teams of workers systematically search for recent gorilla trails, and then follow the trails to the nest sites [Sholley, 1991]. Weaned gorillas build a new nest every night, and leave dung in the nest. The size and composition of the groups are estimated from the nest counts and dung diameter. Typically, at least three of the most recent nest sites of each group are examined to accurately estimate group composition. However, the trails of solitary males and small groups are relatively hard to find, so workers may miss some gorillas altogether [Sholley, 1991; Weber & Vedder, 1983]. In addition, the nest of a blackback (8–12-year-old male) cannot be distinguished from that of an adult female, unless she has an infant >6 months old, which will also leave dung in her nest. The census

techniques do not detect infants <6 months of age, nor can they determine the sex of immature gorillas. To overcome the uncertainties about group composition for unhabituated groups, the census reports use estimates based on the typical proportions of age/sex classes in habituated groups.

Concurrently with the routine censuses, three to five groups of gorillas have been habituated at the Karisoke Research Center for more detailed research, which has provided information about birth rates, mortality rates, dispersal patterns, other life history events, and group structure [e.g., Gerald, 1995; Robbins, 1995, 2001; Sicotte, 2001; Watts, 1990a, 1991, 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]. Mountain gorillas live in groups of two to 40+ individuals (average group size = 10), which typically contain several adult females and their immature offspring, and always contain at least one silverback [Kalpers et al., 2003; Stewart & Harcourt, 1987]. Both males and females may be philopatric or disperse [Harcourt et al., 1976]. Subordinate silverbacks emigrate to become solitary males. Females transfer directly to a solitary male or to another group. Females may transfer multiple times in their lives; however, they usually do not do so with an unweaned offspring, because unrelated males typically kill the infants [Watts, 1989; but see Sicotte, 2000].

Variability in the social system of mountain gorillas is due to the following transitions [Robbins, 1995, 2001; Yamagiwa, 1987; Yamagiwa & Kahekwa, 2001]: New social groups form when females transfer to lone silverbacks. Such groups remain one-male until the male offspring mature into silverbacks, at which time the group is considered multimale. Multimale 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 males have not been observed to take over existing groups.

Although considerable efforts have been made to collect both census and research-group data, relatively few comparisons have been performed to examine whether the population dynamics and social structure of the research groups are representative of the broader population. Census data from the 1970s and early 1980s showed that the growth rate and age structure were reasonably consistent with the estimated birth and mortality rates in the research groups [Harcourt et al., 1981; Weber & Vedder, 1983]. However, it was recently reported that the research-group data predict a higher growth rate than that measured by the censuses (approximately 3% vs. 1%, respectively [Kalpers et al., 2003; Miller et al., 1998; Steklis & Gerald-Steklis, 2001]). The underlying causes of this apparent discrepancy have not been fully explored. In addition, quantitative comparisons between the census and research-group data have not been published for variables relating to social structure, such as the relationship between male emigration patterns, the distribution of silverbacks in groups, and other aspects of group composition.

In this paper, we use an agent-based model to provide a more comprehensive comparison between the census measurements and the research-group data from the mountain gorillas of the Virunga Volcanoes, by simulating many aspects of individual life histories, social group structure, and population dynamics. Agent-based models (or individual-based models) are computer simulations in which individuals are defined by characteristics such as their age, sex, and group affiliation [Kohler & Gumerman, 2000]. The characteristics of an individual change according to predefined rules, such as probabilities for dying, giving birth,

and dispersing. The model tracks each individual over time, while tallying the characteristics of all individuals to quantify the population and social structure. Agent-based models have become increasingly common in studies of population ecology [Grimm, 1999; Lomnicki, 1999], and some of these models have focused on social structure [Cohen, 1975; Pitt et al., 2003]. Other agent-based models have focused more exclusively on relationships between behavior and social structure [Dunbar, 2002; Hemelrijk, 2002]. Our model uses as input data not only mortality and birth rates, but also data regarding female transfers, male emigration, and group fissions. Therefore, the model can predict not only the growth rate and age structure of the population, but also the distribution of gorillas in social groups.

In the ''base simulation,'' we set the input parameters so that the agent-based model would fit the research-group data for birth rates, mortality rates, male emigration, female transfers, and group fissions. We then examined whether the same input parameters would enable the model to match the census measurements for population size and social structure. Particular variables of interest included the growth rate, group size, percentage of immature gorillas in the population, percentage of silverbacks, percentage of multimale groups, percentage of groups containing more than two silverbacks, and the proportion of females in one-male and multimale groups. In the base simulation, some apparent discrepancies emerged, including differences in the growth rate, the percentage of silverbacks in the population, and the distribution of silverbacks in social groups.

For these three discrepancies, we then ran additional simulations to examine how the input parameters could be adjusted to match the census data. Because of the complex relationships among individuals, social groups, and the population structure, several combinations of input parameters could produce comparable simulations of the same census data. Systematic studies of such relationships were beyond the scope of this paper, so here we simply present a small number of simulations, with modifications to each of the most relevant parameters, to illustrate the magnitude of the adjustments that are needed to match each particular variable. For example, to match the growth rate from the census data, we increased mortality rates in one simulation and reduced birth rates in another. By using the research-group data to model the population, and then comparing the results with actual population estimates obtained from the census data, we can explore possible explanations for the discrepancies between the two data sets.

MATERIALS AND METHODS

Overview of the Model

In the agent-based model, each individual is followed over successive time intervals while groups and the overall population structure are also tracked (Fig. 1). To obtain more precise prediction values and a measure of variance, for each simulation we used 500 replicate ''runs,'' from which we calculated the respective means and standard deviations (SDs). Each run spanned 30 simulation years. The initial population (Table I) was based on the results of the 1971–1972 census [Groom, 1973; Harcourt & Groom, 1972; Weber & Vedder, 1983]. Immature gorillas are classified as infants (0–3.5 years), juveniles (3.5–6 years), and subadults (6–8 years). Adult females are >8 years old. Males between the ages of 8–12 years are called blackbacks, and those >12 years old are called adult males or silverbacks [Kalpers et al., 2003; Weber & Vedder, 1983; Sholley, 1991]. Groups are classified as one-male, multimale, and/or all-male, based on their adult composition only.
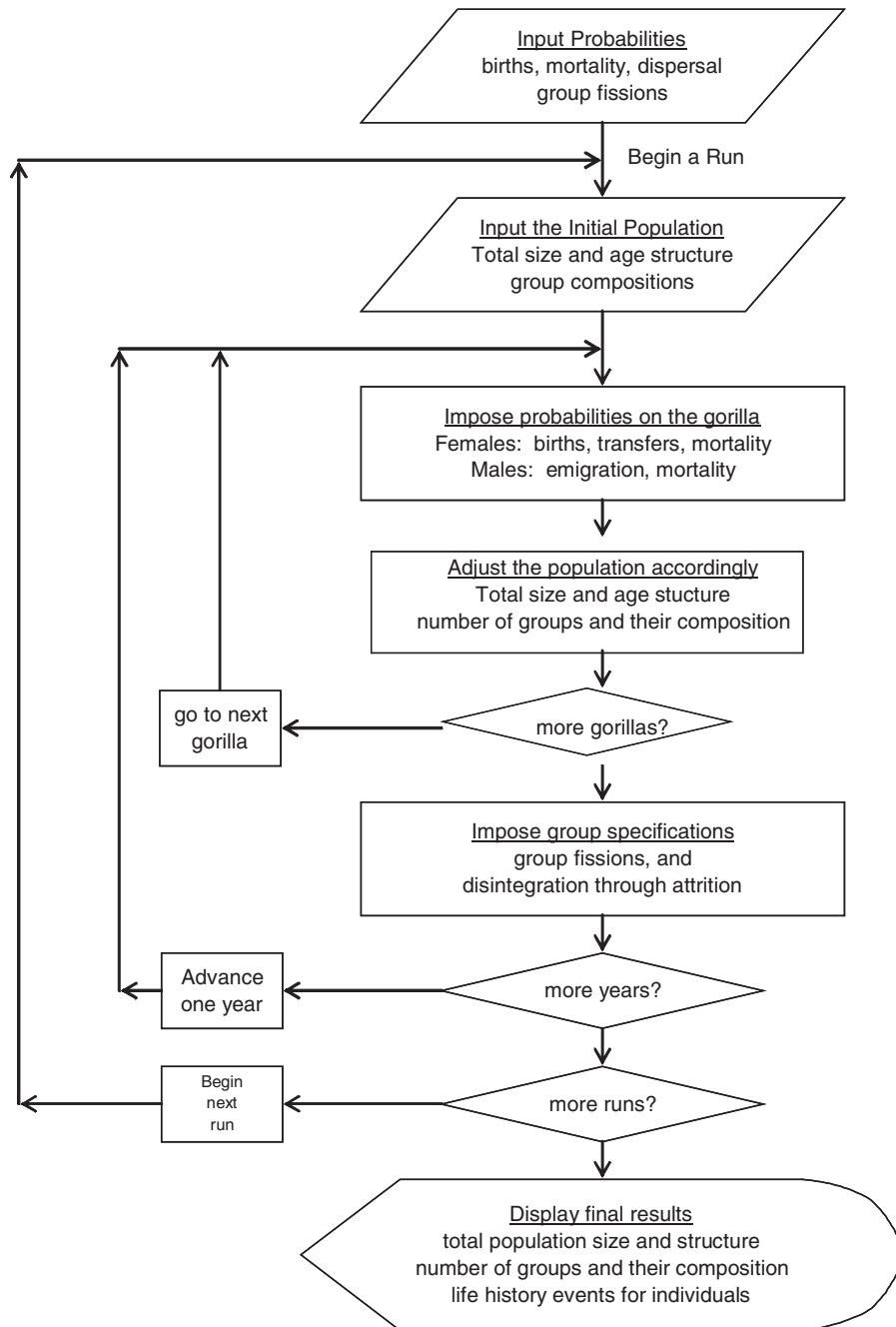
Fig. 1. Flowchart for the agent-based model. The simulations are based on 500 runs of 30 years with 200–700 gorillas.

TABLE I. Summary of the Input Parameters for the Starting Population in the Simulations[*]

Age class	Individuals in each age class	Years in each age class	Individuals/year in each class
Infant	33	3.5	9.4
Juvenile	27	2.5	10.8
Young adult	38	2.0	19.0
Blackback	16	–	–
Silverback	58	–	–
Adult female	89	–	–
Total	261		

Social structure	Initial value
Social groups	31
Mean group size	7.9
Solitary males	15
% Multimale groups	42%
% Immatures in groups	39.8%

[*]The parameters are mainly based upon the 1971–1973 censuses [Groom, 1973; Harcourt & Groom, 1972; Weber & 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, she survives only if the random number is >0.05. If she dies, the model reduces the total population size, her group size, and the number of adult females. The model first evaluates death, then female transfers, births, and male emigration, 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.

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 years, who are randomly assigned to an all-male group or to another lone silverback [Robbins, 1995]. The new silverback also kills all infants <3 years old [Fossey, 1984; Harcourt & Greenberg, 2001; Watts, 1989], the only cause of infanticide that is explicitly considered in the model. 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 (orphan comortality). Interestingly, orphan comortality (unweaned infants dying when their mothers die) has not been discussed as a cause of gorilla mortality in the literature. While more general models of population dynamics would include such deaths in the overall infant mortality probabilities, it is more accurate to model them deterministically, because they depend on female mortality in the same way that infanticide depends on silverback mortality.

We used the agent-based model to run two types of simulations. In the "base simulation," input parameters were based on estimates from observations of the research groups. In subsequent simulations, we changed some of the parameters to adjust for differences between the base simulation predictions and observed population measures from the census data.

TABLE II. Summary of Input Probabilities for the Base Simulation*

IIA: Annual mortality probabilities

Age	Males	Females
0	0.104 (83)	0.115 (78)
1	0.008 (53)	0.058 (53)
2	0.024 (45)	0.001 (45)
3	0.064 (42)	0.073 (42)
4–5	0.024 (36)	0.029 (36)
6–7	0.000 (29)	0.000 (29)
8–11	0.000 (23)	0.014 (23)
12–17	0.025	0.017
18–23	0.022	0.018
24–29	0.157	0.029
30–39	0.104	0.083
40–43	0.400	0.400
44	1.000	1.000

IIB: Constants for the cumulative birth probability Eq. [1]

	a	b	c
Age of first parturition			
One-male groups	14.0	1.2	0.0
Multimale groups	16.0	1.7	0.0
Subsequent birth intervals			
Previous offspring survived	10.0	2.5	0.0
Previous offspring died	15.0	18.0	0.0

IIC: Female transfer probabilities and destination preferences

			Destination preferences		
				Transfer from:	
Transfer probabilities			Transfer to:	OMG	MMG
Natal transfer	0.300		Lone silverback	0.22	0.10
Secondary transfer	0.062		One-male group (OMG)	0.22	0.10
			Multimale group (MMG)	0.56	0.80

*Input parameters were set so the simulation would match reported values from the research groups. IIA: Annual mortality probabilities for each sex at each age (with sample sizes in parentheses when available from the age-specific life table in Gerald [1995]). IIB: Birth probabilities [Gerald, 1995]. IIC: Female transfer probabilities. Transferring females must be at least age six, with no offspring below age three [Sicotte, 2001; Watts, 2000].

Input Parameters for the Base Simulation

For the base simulation, the input probabilities were set so that the model would fit previously reported data from the research groups. The model uses separate mortality probabilities for both sexes at all ages. The input parameters were based upon age-specific life tables for ages 0–11 years, and time-specific life tables for ages 12–40 years [Gerald, 1995]. The model treats some infant mortality deterministically (see above), so we reduced their input probabilities until the model matched the reported values for overall survivorship through those ages. We also added mortality probabilities for ages above 40 years, until no gorillas survived past age 45. Table IIa reflects these adjustments to the previously reported parameters.

Birth probabilities were calculated by

$$P = 1/(1 + \exp[a - b*(t - c)]) \qquad (1)$$

where P is the cumulative probability that a female will have given birth by time "t" (years), and a, b, and c are constants (shown in Table IIb).

This equation produces an S-shaped (or sigmoid) curve that is characteristic of many cumulative probability distributions. When $c = 0$, the ratio a/b represents the (median) time at which the cumulative probability reaches 50%. The steepness of the curves depend upon the magnitude of a and b, relative to "t". The constant "c" shifts the cumulative probability curve forward or backward in time, without changing its steepness. When the model applies Eq. [1] to nulliparous females, "t" refers to the age of the female. For parous females whose previous offspring survived, "t" refers to the years since their last birth. For parous females whose previous offspring died, "t" refers to the years since the offspring died.

The values for a, b, and c were set so the model would match previously reported distributions for a female's age of first parturition, and for the interval between subsequent births. The age of first parturition is earlier for females in multimale groups, and subsequent birth intervals are shorter when the previous offspring dies [Gerald, 1995]. No significant relationship has been observed between birth rate and female group size [Watts, 1990b]. Births in the research groups have not differed significantly from an equal sex ratio (56 males and 41 females, $\chi^2 = 1.2$, $P = 0.28$) [Gerald, 1995], so the model randomly assigns the sex of offspring with a 50% probability of being either male or female.

Subordinate silverbacks in breeding groups are given a 50% emigration probability, at one randomly assigned age between 12 and 18 years, to match the observed proportion of such silverbacks who emigrate [Robbins, 1995]. For all-male groups, the model gives subordinates a 50% probability of emigrating *each year*, because when the research groups were all-male, nine emigrations occurred in 18 subordinate-years [Robbins, 1995].

The model gives an annual transfer probability to females above the age of 6, whenever they do not have a surviving offspring <3 years old [Sicotte, 2001; Watts, 2000]. The model uses two different annual probabilities, depending on whether the female is still in her natal group (Table IIc). When the probabilities indicate that a female will transfer, the model uses a simple weighting function to decide what type of social unit she will enter. For example, the probability that a transferring female will choose a one-male group is

$$\frac{N_{OMG} * FTW_{OMG}}{(N_{OMG} * FTW_{OMG}) + (N_{MMG} * FTW_{MMG}) + (N_{LSB} * FTW_{LSB})} \qquad (2)$$

where N_{LSB}, N_{MMG}, and N_{OMG} are the number of lone silverbacks, multimale 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 IIc). The weighting factors were set so that the base simulation model would match previously reported proportions for the destinations of female transfers [Watts, 2000]. To describe the female distribution in groups that results from such transfers, we define a "female group

distribution ratio'' as

$$FGDR = \frac{\text{(average number of adult females in a multimale group)}}{\text{(average number of adult females in a one-male group)}} \quad (3)$$

Five group fissions have been reported for the approximately 100 multimale-group years that habituated groups have been followed [Kalpers, 2003; Robbins, 1995], so the model uses a 5% probability that a multimale group will fission in a given year. A multimale group must have at least five members before the model will apply that probability. For purposes of computation expediency, fission automatically occurs in the very rare cases in which a multimale group has more than 90 members at the end of a year. During fissions, the model randomly gives the resulting new group 10–50% of the members from the parent group. At ages of 0–4 years, gorillas stay with their mothers during fissions.

Input Parameter Adjustments to Match Census Data

In addition to the base simulation, for which the input parameters were set to match the research-group data, we ran other simulations for which the input parameters were set to match a specific variable from the census data (Table III).

TABLE III. Adjustments to the Input Parameters for Each Simulation

Simul-ation	Description	Adjustments to the input parameters (in comparison with the base simulation)
1	Base simulation	
	Lower growth rate	
2	Lower birth rates	In Equation [1], parameter ''c'' = 1.5 for all four birth types.
3	Higher mortality	Multiplied all mortality probabilities by 1.5.
	Higher male mortality	
4	All males	Multiplied mortality probabilities by 2.4 for males, and 1.5 for females.
5	All SB	Multiplied mortality probabilities by 3 for all SB, and 1.5 for all other gorillas.
6	All LSB	Multiplied mortality probabilities by 100 for LSB, and for 1.5 all other gorillas.
	Male emigration	(also with mortality probabilities multiplied by 2.4 for males, and 1.5 for females.)
7	100% probability	All subordinate SB emigrate, but not until their randomly designated age between 12–18.
8	Only at age 12	All emigration occurs at age 12, and they have the standard 50% emigration probability.
9	When 3+ SB	SB emigrate at their designated age, if and only if their group has at least two other SB.
10	Combination case	Multiplied mortality probabilities by 1.4 for females, 2.0 for SB, and 1.8 for other males. Emigration probabilities = 20%, 80%, and 100% in groups with 2, 3, and 4+ SB, respectively, at randomly designated ages between 12–15.

SB, Silverback; LSB, lone silverback.

First, we focused on reducing the growth rate in the model so that it would equal the observed rate from the census data. Simulation 2 shifts the cumulative birth probability distribution in Eq. [1] by 1.5 years, effectively delaying all births by an average of 18 months. Alternatively, in simulation 3, we inserted a 1% probability for those ages with a 0% mortality probability, and then multiplied the mortality probabilities by 1.5 for all age/sex classes. Unless otherwise stated, we maintained these mortality adjustments in all subsequent simulations. When the probabilities exceed 100%, the model treats them the same as it does 100%.

To match the observed proportion of silverbacks in the population, we ran three simulations that increased mortality for all age/sex classes, with additional mortality adjustments for an increasingly narrow segment of the male population. In simulation 4, we multiplied the annual mortality probabilities for all males and females by 2.4 and 1.5, respectively (in comparison with the base simulation). In simulation 5, we multiplied the annual mortality probabilities for all silverbacks by 3.0, and for all other male and female ages by 1.5. In simulation 6, silverbacks died if they were still solitary 1 year after emigration (100% mortality). All other male and female annual mortality probabilities were multiplied by 1.5.

To match the observed proportion of multimale groups with more than two silverbacks, we ran three simulations with different emigration patterns for subordinate silverbacks in breeding groups. These simulations also maintained the higher mortality probabilities from simulation 4. In simulation 7, all silverbacks emigrated if they had not become dominant before their randomly selected age (12–18 years). In simulation 8, all emigration occurred at age 12, with the standard 50% probability from the base simulation. In simulation 9, subordinates emigrated at their randomly selected age, but only if their group contained at least two other silverbacks.

Simulation 10 combined several types of adjustments to the previous simulations (Table III). To match the growth rate, we again adjusted mortality rates for all gorillas (as in simulation 3). To reduce the discrepancy in the number of silverbacks, we made separate adjustments for the mortality of silverbacks and other males (a hybrid of simulations 4 and 5). To reduce the discrepancy in the proportion of multimale groups with more than two silverbacks, we adjusted both the age range for emigration (similar to simulation 8) and the way in which the emigration probabilities depended on the number of silverbacks in the group (similar to simulation 9).

RESULTS

Comparison Between the Base Simulation and the Research-Group Data

The results from the base simulation closely match the values for the demographic data obtained from the research groups (Table IV). In the model, most of these values are directly related to specific input parameters, so while the accurate results may support the general validity of the model, they mostly confirm that we set the input parameters appropriately. For example, the predictions confirm that we set the mortality probabilities to match the reported values for survivorship (Fig. 2), and that we set the parameters in Eq. [1] to match the distribution of ages for first parturition, and the intervals for subsequent births (Fig. 3).

TABLE IV. Comparison of the Base Simulation With Long Term Demographic Data for Life History Events and Group Transitions*

	Base simulation	Research groups	Details for research group data
Birth and death rates			
Deaths/gorilla/year	0.049	n.r.	
Births/gorilla/year	0.079	n.r.	
Births/adult-female/year	0.264	0.28[a]	55 births in 195 female-years
Infanticide			
% of infant mortality	28%	26%[b]	5 of 19 deaths, 95% C.I. = 9–51%
% of all births	8%	10%[b]	5 of 50 births, 95% C.I. = 3–22%
Orphan co-mortality			
% of infant mortality	23%	n.r.	
% of all births	6%	n.r.	
Age of first parturition			
One-male groups	11.1	11.1[c]	8 births, standard deviation = 1.3 years
Multimale groups	9.9	9.9[c]	22 births, standard deviation = 1.1 years
Inter-birth intervals in years (IBI)			
Previous offspring survives	4.0	3.9[c]	62 births, standard deviation = 0.7 years
Previous offspring dies	2.2	2.0[c]	39 births, standard deviation = 1.1 years
% of IBI after offspring dies	30%	39%[c]	39 of 101 births, 95% C.I. = 29–49%
Dispersal frequencies			
Male emigration	40%	36%[d]	4 of 11 emigrated, 95% C.I. = 11–69%
Natal female transfer	64%	65%[e]	12 of 19 transferred, 95% C.I. = 38–84%
Secondary female transfer	0.63	0.63[e]	15 transfers among 24 females
Proportion of transferring females who entered multimale groups			
From multimale groups	73%	60–93%[f]	12 of 20 transfers, or 13 of 14
From one-male groups	48%	41–49%[f]	15 of 37 transfers, or 11 of 23
Group transitions			
Fissions	0.045	0.05[d,g]	5 fissions in 100 multimale group-years
Disintegrations	0.044	0.05[d]	4 disintegrations in 78 total group-years

*Values for infanticide reflect only the cases that occur during group disintegration.
[a]Steklis and Steklis [2001].
[b]Fossey [1984]; Watts [1989].
[c]Gerald [1995].
[d]Robbins [1995].
[e]Sicotte [2001].
[f]Two sets of data in Watts [2000].
[g]Kalpers et al. [2003].
C.I., confidence intervals; n.r., not reported.

Comparison Between the Base Simulation and the Census Data

The base simulation predicts an average growth rate of 3.1%, which is substantially higher than the actual growth rate of 1.2% over the past three decades [Kalpers et al., 2003] (Fig. 4a). As the actual population has grown, the average group size and the number of groups have both increased, but neither trend has been consistent (Fig. 4b). The model predicts that the population
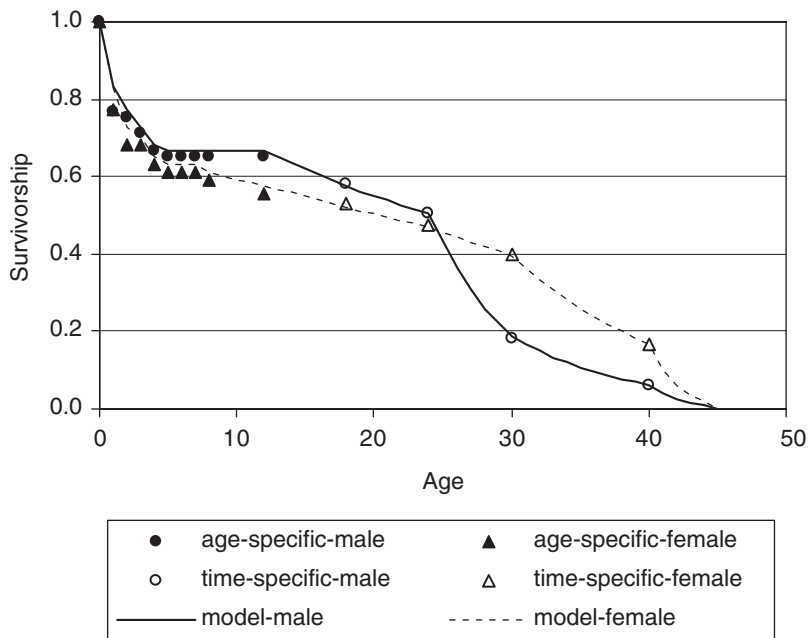
Fig. 2. Survivorship curves for male and female mountain gorillas. Input parameters for the base simulation were set so that the results would match the life tables published by Gerald [1995].

growth will be reflected mainly by an increase in the number of groups. Despite the unrealistic growth rate, the predictions for the average and range of group size remain within the range of observed values, although average group size and its variance increase. The biggest discrepancy arises with very small groups (Table V). The simulation predicts that 25% of all groups will have only two or three members. In the three censuses for which data are available, only 10 of the 92 groups were that small (mean = 11%, 95% confidence interval = 5–19%). On the other end of the size distribution, the model predicts that 0.5% of the groups will exceed 47 members, the largest size reported so far in the censuses [Kalpers et al., 2003]. In over 500,000 simulated group-years, only three groups reached the computational size limit of 90 gorillas.

The census data for age structure and group structure (percent multimale groups) did not show consistent trends over time (Fig. 5a and b), and the predicted values generally fell within the range of observations (but see below for silverbacks). We did not attempt to mimic the particular fluctuations in the observed age and group structure. Nonetheless, the predicted values fluctuated due to an inverted age structure in the initial population. In the first year, the simulations reflected census data, with an average of 19 subadults but only nine infants at each age (Table I). As the initially high proportion of subadults advanced into maturity (1972–1974), the predicted percentage of immatures dropped. When the initially low proportion of infants reached the age at which they became silverbacks (1984–1986), the predicted percentage of multimale groups reached its minimum (Fig. 5b). Thus, the simulation shows how the inverted age structure in the first year can partially explain some of the subsequent fluctuations.

As the base simulation approached a stable age structure, it overestimated the proportion of silverbacks by 30–35% (Fig. 5a). In the simulation, many of the
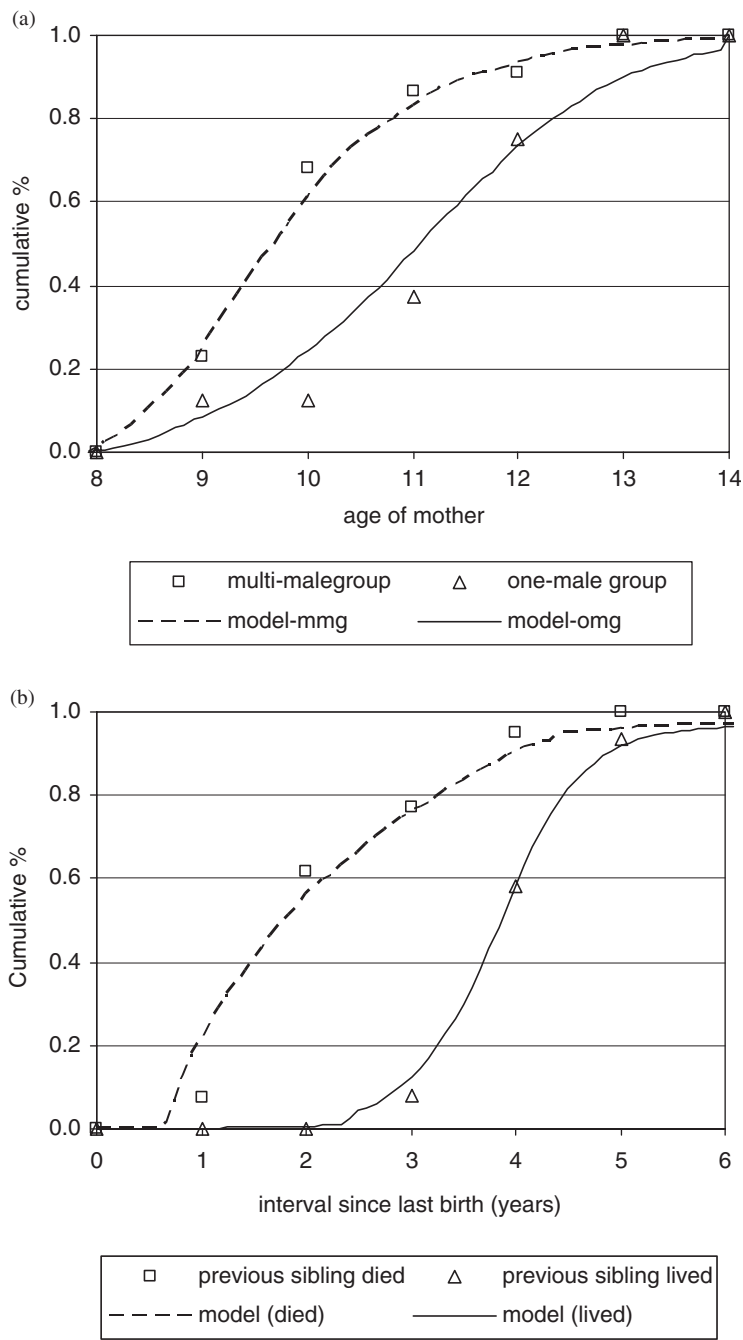
Fig. 3. Comparison of the long-term demographic data with the base simulation for the cumulative percentage of each type of birth: (**a**) age at first birth for females in one-male groups (OMG) and multimale groups (MMG), and (**b**) interbirth intervals.
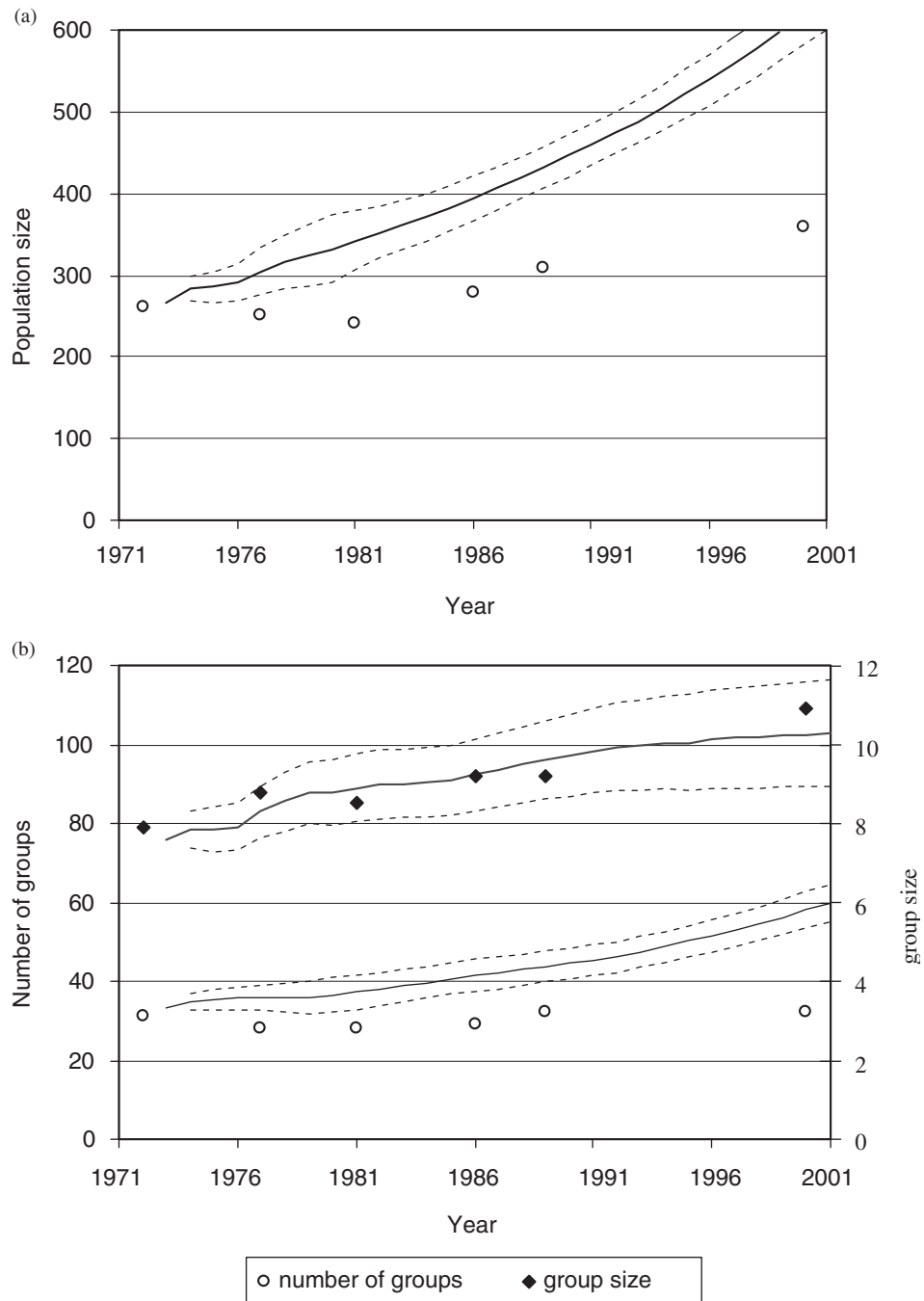
(a)

(b)

○ number of groups   ◆ group size

Fig. 4. Dynamic simulation of (**a**) the population size and (**b**) average group size and number of groups. Points are from the census data. The solid line is the base simulation average, and the dashed lines are the SD.

**TABLE V. Effect of Demography and Behavior on the Population Size, Age Structure, and Social Structure*

No.	Description	Growth Rate	% Immatures	% SB	Multimale groups % of all Groups	% with 3+ SB	Group Size	Groups with 2–3 members	Female distribution ratio	Disint/ grp/yr	I'cide/births
	Actual data	1.2%	42.3%	17.9%	34%	18%	9.3	11%	1.8	0.05	10%
	References		a–f	a,b,e,f	a–f	b,e,f	a–f	b,e,f	b,e,f	g	h,i
1	Base simulation	3.1%	42.1%	21.4%	37%	43%	9.0	25%	2.0	0.044	8%
	Lower growth rate										
2	Lower birth rates	**1.2%**	36.3%	23.8%	36%	38%	7.6	29%	1.9	0.048	9%
3	Higher mortality	**1.2%**	41.5%	21.2%	35%	37%	8.6	25%	1.8	0.062	11%
	Higher male mortality										
4	All males	0.6%	42.2%	**17.8%**	33%	34%	10.0	21%	1.7	0.087	15%
5	All SB	0.7%	42.5%	**17.7%**	34%	38%	10.6	20%	1.7	0.095	17%
6	All LSB	1.2%	42.7%	**17.9%**	44%	42%	11.1	13%	1.7	0.053	9%
	Male emigration										
7	100% probability	0.3%	41.9%	18.0%	25%	**24%**	9.0	24%	1.4	0.099	19%
8	Only at age 12	0.4%	42.1%	17.9%	26%	**26%**	9.2	24%	1.5	0.095	18%
9	When 3+SB	0.7%	42.4%	17.7%	34%	**24%**	9.8	21%	1.6	0.083	14%
10	Combination case	1.1%	42.3%	19.1%	31%	22%	9.0	24%	1.7	0.075	14%

*Values in bold highlight the results that the simulations were directly intended to adjust. Census data are averages from all years where the value was reported; simulation values are the average of those same years. a: 1971–1973; b: 1976–1978; c: 1981; d: 1986; e: 1989; e: 2000; g: Robbins [1995]; h: Fossey [1984]; i: Watts [1989]. SB, silverback; LSB, lone silverback; Disint, group disintegrations per total group-years; I'cide, infanticide as a percentage of total births.
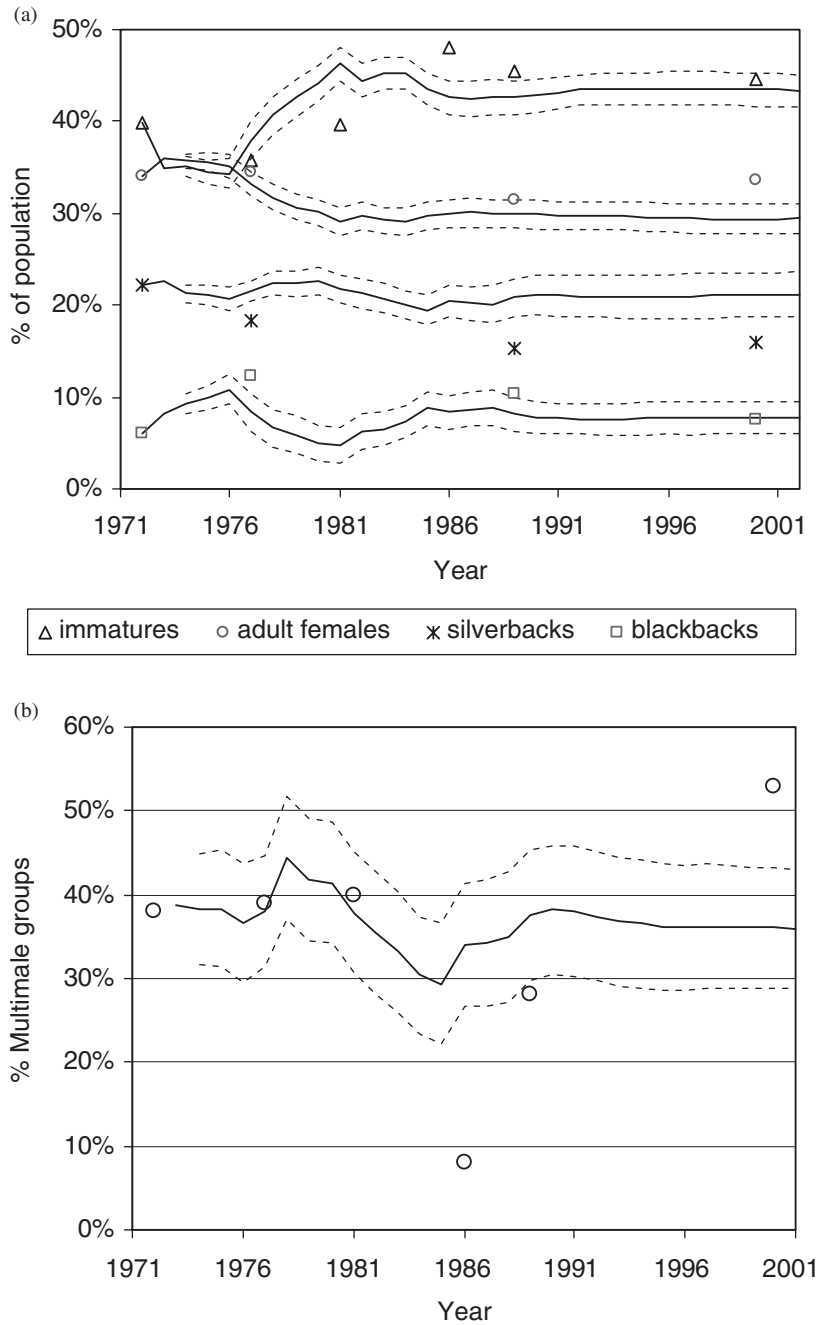
(a)

△ immatures   ○ adult females   ✳ silverbacks   □ blackbacks

(b)

Fig. 5. Dynamic simulation of the (**a**) age structure and (**b**) percentage of groups with more than one silverback. Points are from the census data. The solid line is the base simulation average, and the dashed lines are the SD.

''extra'' silverbacks were in multimale groups. The simulation predicts that 41% of multimale groups will have more than two silverbacks (Table V). Of the 28 multimale groups whose composition was reported in the census data, only five had more than two silverbacks (mean = 18%, 95% confidence interval = 6–37%). The female group distribution ratio (Eq. [3]) ranges from 1.5 to 2.7 in the census data, compared with values of 1.7–2.5 in the base simulation (Table V). This agrees with the observation that multimale groups typically contain more adult females than one-male groups [Robbins, 1995; Steklis & Gerald-Steklis, 2001].

Simulations to Match Census Data

To match the growth rate observed in the censuses, we decreased the birth rate in simulation 2 by 30% (from 0.26 to 0.18 births/adult female/year). Alternatively, in simulation 3, we increased the overall mortality rate by 50% (from 0.05 to 0.075 deaths/gorilla/year). The magnitude of these adjustments is not surprising, since the birth rate was 60% higher than the death rate in the base simulation (Table IV). Higher mortality rates had little impact on the age and group structure, but when we reduced birth rates, the average group size and percentage of immatures in the population declined much more (Table V). Both simulations fulfilled our goal of matching the observed growth rate; however, simulation 2 created more discrepancies with the age and social structure than did simulation 3. Therefore, we chose to increase mortality rates, rather than reduce birth rates, in all subsequent simulations.

To match the observed percentage of silverbacks in the population, in simulation 4 we increased the mortality rate for all males to 0.112 deaths/ year—more than double the base simulation. In simulation 5, we increased the mortality rate for all silverbacks to 0.116 deaths/year, which is again more than double the base simulation. In comparison, from 1967 to 1992, the research groups experienced nine silverback deaths in 135 silverback-years (mean = 0.067 deaths/silverback/year, 95% confidence intervals ~0.03–0.12 [Robbins, 1995]). In both simulations, the predictions improved slightly for the percentage of very small groups, the percentage of multimale groups remained the same, and the average group size increased. In simulation 6, in which all lone silverbacks died within 1 year of emigration, the model showed the biggest overestimates for average group size and the percentage of multimale groups, and its closer fit for very small groups is questionable (see Discussion). In simulations 4 and 5, higher male mortality was also reflected in higher rates of group disintegration and infanticide, which reduced the growth rate compared to simulations 2 and 3.

In simulations 7–9, no single adjustment of male emigration was sufficient to exactly match the observed proportion of multimale groups with more than two silverbacks. In all three simulations, however, the predictions improved enough to fall within the 95% confidence intervals of the census data (above). The predictions for average group size matched the census data in all three simulations as well. The percentage of multimale groups declined in simulation 7, but remained within the range of observed values even though all of the silverbacks that remained subordinate eventually emigrated. When all emigration occurred while the subordinate was age 12 in simulation 8, the results were similar to those from simulation 7. By making emigration rates dependent on the number of other silverbacks in the group, simulation 9 maintained the most accurate overall percentage of multimale groups in the population.

In most simulations with selectively higher male mortality rates (simulations 4, 5, and 7–9), the growth rate declined below the census value, mainly because of

higher rates of group disintegration and infanticide (Table V). Therefore, to match the observed growth rate in these simulations, the mortality probabilities would not need to be increased as much as they were (relative to the base simulation). Simulation 10 illustrates such further refinements of mortality, along with a hybrid of adjustments for male emigration. The final simulation closely matches the growth rate from the census data, but it deliberately retains some differences with the less reliable measurements for silverbacks and very small groups. The simulation still predicts slightly too many groups with more than two silverbacks, but its input assumptions are less extreme than those of simulations 7–9.

DISCUSSION

The input parameters for the base simulation were set so that its predictions would match many aspects of the long-term demographic data from the research groups (i.e., rates for birth, mortality, male emigration, female transfers, and group fissions; Table IV). With these input parameters, the simulation did not closely match the main aspect of the census data: the total population size and growth rate. Nonetheless, its predictions generally fell within the range of observed values for the average group size, the percentage of multimale groups, and the distribution of females among groups. Additional discrepancies arose, however, in the percentage of silverbacks in the population, the proportion of multimale groups with more than two silverbacks, and the proportion of groups with only two or three members (Table V). There are four possible reasons why the simulations showed these apparent discrepancies between the research-group data and the census data: 1) the research groups may differ from the broader population, 2) the data set from the research groups may not be sufficiently complete to reflect population-wide demographic patterns, 3) the census data may not be completely accurate, and 4) the model may be too simplistic. These explanations are discussed below.

The discrepancy in growth rate between the census measurements and the research-group data probably occurred because these groups have indeed grown more rapidly than the overall population. For example, in the 2000 census, essentially all of the population growth for the previous decade occurred in the three research groups plus one neighboring tourist group [Kalpers et al., 2003]. The census counts are reportedly accurate to within 5–10%, so they should provide a reliable measure of the balance between birth and death rates in the entire population. Thus, the main question is whether the discrepancy is a result of different birth rates, different mortality rates, or some combination of the two. The literature provides support for either conclusion. The research groups have received better protection from poachers [Steklis & Gerald-Steklis, 2001; Plumptre & Williamson, 2001], they have received veterinary care in emergency situations [Mudakikwa et al., 2001], and they experienced a much shorter period of heavy disturbances during the recent civil unrest [Kalpers et al., 2003]. All of these differences are likely to affect mortality more than birth rates. The research groups occupy some of the best feeding habitats [McNeilage, 1995, 2001], which could support a higher birth rate to recover from the human disturbances. Better nutritional conditions are expected to enhance reproductive output [Bentley, 1999]. The research groups have had a slightly higher birth rate than the groups habituated for tourism, but the difference is not statistically significant [Steklis & Gerald-Steklis, 2001].

Our simulations indicate that the discrepancy arises primarily because of a greater difference in mortality rates, because the predicted percentage of immatures dropped much further when we adjusted birth rates instead (simulations 2 and 3). The initial censuses had a lower percentage of immatures, which may suggest lower birth rates and poorer feeding ecology while the park was still overrun with cattle [Curry-Lindahl, 1969; Harcourt & Fossey, 1981; Weber & Vedder, 1983]. However, the cattle were removed in the mid 1970s, and most subsequent fluctuations in the population appear to reflect poaching and civil unrest.

When the simulations matched the observed growth rate, the percentage of silverbacks in the population remained too high by 30–35%, a difference of about 15–20 adult males. Census techniques have been reported to undercount solitary males by about 50%, which would reduce the apparent discrepancy by three to six males [Weber & Vedder, 1983]. The remaining discrepancy probably arose because the research-group data are still too limited to reflect the mortality rates of the overall population. Indeed, no mortality has yet been observed in males between the ages of 6 and 11. In the research groups, survivorship through age 12 has been 25% higher for males than females, but such differences are not statistically significant [Gerald, 1995]. Even when we doubled mortality for silverbacks in simulation 5, the simulation still fell within the 95% confidence intervals of the research-group data for silverback mortality. The wide confidence intervals illustrate that the research data are not yet sufficiently complete to provide precise predictions about population structure. Accurate estimates of mortality for long-lived species are notoriously difficult to obtain [Gaillard et al., 1998].

Higher mortality has been estimated for dispersing males of other species, for reasons such as higher male–male aggression, increased risk of predation, and less familiarity with food resources in their new area (e.g., baboons [Alberts & Altmann, 1995] and dwarf mongooses [Lucas et al., 1997]). However, the simulations did not suggest that the discrepancy in the proportion of silverbacks was due to higher mortality for lone silverbacks. When we selectively increased mortality for lone silverbacks, simulation 6 showed the worst simulation of the population and social structure. Furthermore, in order to match the overall percentage of silverbacks in the census data, the simulation had to assume that solitary males survive only 1 year after they emigrate. This assumption seems extreme compared to the long-term demographic data in which at least two lone silverbacks are known to have survived for 4–6 years [Robbins, 1995]. Unfortunately, however, solitary males have not been regularly monitored, so although some known emigrants were occasionally observed years afterward, the fate of most is unknown. Mountain gorillas have abundant food and no longer have natural predators, so male–male aggression would be the most likely cause of the higher mortality in lone silverbacks. It seems plausible that solitary males are less competitive and experienced than silverbacks in groups (otherwise they would not still be solitary), but the stakes are high for both solitary males attempting to acquire females, and silverbacks in established groups who want to retain females. More empirical data are needed before we can understand the differences in mortality between solitary and group-living silverbacks.

The third discrepancy we tried to address was that simulations 1–6 had too many multimale groups with more than two silverbacks. The census reports did not mention any difficulty in measuring this aspect of the social structure, but if subordinate males nested on the periphery of the group, it is possible that their nests were undercounted (personal observation). The discrepancy may also arise

if the research groups provide an underestimation of male emigration rates and are not representative of the overall population. Of the three simulations that focused on this discrepancy, the best predictions arose when we assumed higher emigration for silverbacks who face more competition within their group (simulation 9). That simulation is qualitatively consistent with studies of male baboons, who are significantly more likely to emigrate from groups with a high number of competitors [Alberts & Altmann, 1995], and previous analyses have suggested similar dispersal patterns for mountain gorillas [Robbins, 1995; Watts, 2000]. Further studies of silverbacks are under way to examine how optimal dispersal strategies depend on the number of males and females in a group, the ages of the dominant and subordinate males, and the degree of reproductive skew [Robbins & Robbins, unpublished results].

Throughout the previous simulations, the predicted proportion of very small groups (two or three members) remained higher than the census data. The occurrence of very small groups is useful for elucidating methods of group formation (females transferring to lone silverbacks and group fissions) and disintegration. Although the discrepancy seems relatively large in the base simulation, it represents only about three or four groups for each census. Sholley [1991] acknowledged the likelihood that ''a few'' very small groups may not have been detected in the 1989 census. Therefore, this apparent discrepancy probably arises from inaccuracies in this aspect of the census measurements. Little is known about the process of group formation, but the low number of very small groups observed in the population suggests that our modeling of female transfers to lone silverbacks and small groups may have been too simplistic. For example, particularly successful males may acquire many females simultaneously, especially since females sometimes transfer jointly [Sicotte, 2001].

In nearly all of the simulations with selectively higher male mortality rates, the growth rate declined below the census value, due to higher rates of group disintegration and infanticide (Table V). These results illustrate how social structure can influence predictions for population dynamics, and they reflect complex relationships among individual life history events, group composition, and the population age structure. The growth rate is influenced by group disintegration and infanticide, which depend on male mortality and the percentage of multimale groups, which in turn are related to patterns of male emigration and group fissions. In the base simulation, the predictions for group disintegration and infanticide are comparable to the early research-group data, when the groups were more representative in size and structure of the overall population [Watts, 1989; Weber & Vedder, 1983]. Since that data set was published, however, the research groups have been almost entirely multimale, and none has disintegrated, so there have been no further opportunities for such infanticide [Kalpers et al., 2003; Robbins, 1995, 2001]. An increase in male mortality leading to an increase in infanticide, which in turn affects the birth rate and population growth rate, has also been observed in lions [Packer & Pusey, 1983] and black bears [Swenson et al., 1997; Wielgus et al., 2001].

Simulation 10 adjusts for these relationships, and draws together the insights from the preceding simulations, by making a composite of adjustments for mortality and male emigration to address the main discrepancies with the census and research-group data. Simulation 10 is not meant to be a definitive interpretation of the actual life history of the gorillas living in the Virunga Volcanoes region, and other combinations of parameters would probably produce comparable results. We present it as an example of what is needed to match the census data more realistically than the base simulation.

In conclusion, the base simulation highlighted some discrepancies between the research-group data and the census measurements, and additional simulations have begun to help us resolve those discrepancies. This study emphasizes the importance of comparing census results against the accuracy of estimates from selected research groups to best understand population dynamics [Haydon et al., 1999]. Simulations cannot replace the need for more empirical data, but they enhance our understanding of the data that are already available. The agent-based model used in this study could easily be modified to simulate the life history events and demographic patterns of other social species.

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