Assessing reintroduction success in long-lived primates through population viability analysis: western lowland gorillas *Gorilla gorilla gorilla* in Central Africa

T O N Y K I N G , C H R I S T E L L E C H A M B E R L A N and A M O S C O U R A G E

Abstract The use of population modelling has become an increasingly common tool in reintroduction planning and assessment. Although initial reintroduction success is often measured by quantifying post-release survival and reproduction, longer-term success is best assessed through measurements of population viability. Here we develop a population model capable of providing useful results for influencing management of a reintroduction programme for a long-lived and slow-reproducing primate, the western lowland gorilla *Gorilla gorilla gorilla*. We used post-release monitoring data from two reintroduced populations in the Batéké Plateau region of Congo and Gabon, complemented with published data on wild and captive populations, to develop a population model using *Vortex*. Sensitivity testing illustrated that the model was highly sensitive to changes in the input parameters for annual birth rates, the number of lethal equivalents, and for female annual mortality rates, especially for adults. The results of the population viability analysis suggested that the reintroduced gorilla populations have a reasonable chance of persistence ($>$ 90% over 200 years) but illustrated that reinforcement of the populations could significantly improve probabilities of population persistence and retention of genetic diversity. Equally, catastrophic events could have significant negative impacts. Continued monitoring of the populations should allow refinement of the model, improving confidence in its predictions and its relevance to decision-making.

Keywords Batéké Plateau, Congo, Gabon, *Gorilla gorilla gorilla*, population model, post-release monitoring, rehabilitation, reintroduction management

Introduction

The use of population modelling is becoming an increasingly common tool in reintroduction planning

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and assessment (South et al., 2000; Armstrong & Ewen, 2002; Armstrong & Reynolds, 2012; Parlato & Armstrong, 2012). Population models can be particularly helpful in assessing reintroduction success. Although initial reintroduction success is often measured by quantifying post-release survival and reproduction (Britt et al., 2004; Goossens et al., 2005; Maran et al., 2009; Tavecchia et al., 2009; King et al., 2012), the ultimate goal of a reintroduction is to re-establish a viable, self-sustaining population (IUCN, 2002; Beck et al., 2007). The probability of the long-term persistence of a re-established population is best measured through modelling of population viability (Seddon et al., 2007, 2012). Another major role of population models is in guiding reintroduction decision-making (Armstrong & Reynolds, 2012), including assessing potential reintroduction sites (Cramer & Portier, 2001; Schadt et al., 2002) or potential release stock (Robert, 2009), estimating the number of release stock necessary or the required duration of the release period (Slotta-Bachmayr et al., 2004; Armstrong & Seddon, 2008; Gusset et al., 2009; Schaub et al., 2009), evaluating the impacts on the source population (Bustmante, 1996; Somers, 1997; Todd et al., 2002; Kohlmann et al., 2005; Dimond & Armstrong, 2007), and comparing potential management strategies (Armstrong et al., 2007; Wakamiya & Roy, 2009; Martínez-Abraín et al., 2011).

Population viability models are, however, highly sensitive to the quality of the input data (South et al., 2000; Asbjørnsen et al., 2005). Accurate estimations of demographic parameters are particularly difficult to obtain for long-lived species (Harcourt, 1995; Gaillard et al., 1998; Robbins & Robbins, 2004), and for the majority of reintroduced populations of any species because of low sample sizes (Nichols & Armstrong, 2012). Consequently reintroduction programmes for several long-lived primate species (e.g. Yaeger, 1997; Tutin et al., 2001; Goossens et al., 2005; Strum, 2005; King & Courage, 2008; Peignot et al., 2008) have yet to utilize population viability models in planning or assessment. A review of literature on modelling reintroduced populations (Armstrong & Reynolds, 2012) analysed 89 papers, of which 46 concerned mammals but only one concerned a primate (Swart & Lawes, 1996). This may to some extent be because of the geographical bias of publications, with most relating to projects in Europe, North America, New Zealand or Australia, where primates do not occur, and many models may not be published

(Armstrong & Reynolds, 2012). The model we develop here, for reintroduced western lowland gorillas *Gorilla gorilla gorilla*, appears to be the first published attempt to assess the long-term viability of a reintroduction programme for a long-lived and slow-reproducing threatened primate.

The western lowland gorilla is categorized as Critically Endangered on the IUCN Red List (Walsh et al., 2008) based on a projected 80% decline in the wild over three generations. The major causes of decline are commercial hunting and mortality caused by the Ebola virus (Tutin et al., 2005; Walsh et al., 2008), with habitat loss and degradation, and possibly climate change, expected to become major threats (Walsh et al., 2008). Gorillas can live for > 40 years, usually do not reproduce until they are at least 10 years old, and females produce only one surviving offspring about every 5 years (Harcourt & Stewart, 2007).

Two populations of western lowland gorillas are in the process of being re-established in the Batéké Plateau region of central Africa, one each in the neighbouring countries of the Republics of Congo and Gabon (King, 2004; King & Courage, 2007, 2008; Pearson & King, 2008). The first releases occurred in 1996 and 2001, respectively, in the two countries, and post-release monitoring data have recently been analysed to quantify demographic parameters, to allow an assessment of initial reintroduction success (King et al., 2012). This analysis illustrated that the reintroduction programme had been successful in terms of post-release survival, reproduction, and dispersal, with quantitative measures of these parameters being similar to comparable measures for wild populations (King et al., 2012). To assess longer-term success we use the demographic data for the reintroduced populations (King et al., 2012) and published data on wild and a few captive gorilla populations to develop a population model. We use the model to investigate how possible scenarios could affect the viability of the two reintroduced populations, and how population models can inform reintroduction management decisions for long-lived species.

Methods

Study populations

The two reintroduced western lowland gorilla populations are located in the Lesio-Louna Reserve of Congo and the Batéké Plateau National Park of Gabon (Fig. 1). Pre-release preparations and release implementation are described elsewhere (King et al., 2012). Both reintroduction sites have collaborative protected area management projects that arose from the development of the reintroduction programme, and the sites and the reintroduced populations have benefited from long-term post-release monitoring and surveillance (King, 2008; King & Courage, 2008; King et al., 2012).
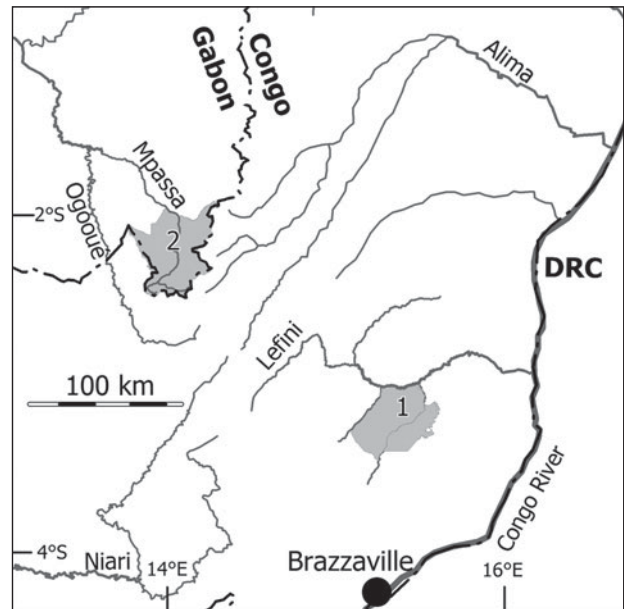

FIG. 1 The location of the two gorilla reintroduction sites (grey shading): the Lesio-Louna Reserve in Congo (1) and the Batéké Plateau National Park in Gabon (2), with major rivers and country borders.

Consequently, hunting pressure, which was identified as the main cause of the local extirpation of gorillas, has been dramatically reduced (King, 2008; King et al., 2012). A total of 51 gorillas (24 males, 27 females) were released between 1996 and 2006, 25 in Congo and 26 in Gabon, comprising 43 rehabilitated wild-born orphans, and one in situ and seven ex situ captive-born (King et al., 2005, 2009, 2012). In April 2009 total population sizes were 23 in Congo (comprising 15 wild-born and one in situ captive-born aged 8–22 years, plus seven first-generation offspring aged 6 months–5 years) and 25 in Gabon (16 wild-born and six ex situ captive-born aged 7–13 years, plus three first-generation offspring aged 2 months–1.5 years). Further releases are expected at both sites (King & Courage, 2008).

Population modelling

We used *Vortex v. 9.94* (Lacy et al., 2003) to develop the population model for the reintroduced gorilla populations. *Vortex* is appropriate for modelling species with low fecundity and long lifespans (Miller & Lacy, 2005) and is the most commonly used software in published reintroduction models (Armstrong & Reynolds, 2012).

The demographic input parameters we used were based primarily on a combination of the results of the post-release monitoring of both reintroduced gorilla populations (King et al., 2012), compared with data on wild, or occasionally captive, western and eastern *Gorilla berengei* gorillas (Table 1). The calculation of some input parameters required further analysis of the post-release monitoring data from the

TABLE 1 Parameters used for modelling populations of the western lowland gorilla *Gorilla gorilla gorilla* in the Lesio-Louna Reserve of Congo and the Batéké Plateau National Park of Gabon (Fig. 1), with the demographic input values used in the baseline scenario, values for the reintroduced populations based on post-release monitoring results, and rationale for the choice of each input value.

Parameter	Value used for baseline scenario	Value in reintroduced population	Rationale
Mate monopolization (% of adult males in breeding pool)	28.6% (=1 per 3.5 females)		Studies of 5 wild populations of western gorillas found median number of adult females per predominantly single-male breeding group to be 3.5 (range of population means 2.9–7.1; Harcourt & Stewart, 2007).
Annual birth rate	0.20	0.196[1]	0.20, represented as 20% of adult females available to breed each year, with a maximum of 1 offspring per female per year, is similar to the rates given by King et al. (2012) for reintroduced populations (0.196), & by Robbins et al. (2004) for 2 wild populations of western gorillas (0.198, 0.180), & for mountain gorillas (0.226).
Environmental variability in annual birth rate	2.4%	2.4%[2]	Corresponds to the SD of annual birth rates in the reintroduced populations unaccounted for by the expected SD because of demographic stochasticity.
1st age of breeding for females	10 years	8.6–16.8 years (median 10.3, mean 11.6)[1]	10 years reflects data for reintroduced populations; although not measured in wild western gorillas (Robbins et al., 2004), female mountain gorillas, considered sexually mature from 8 years old, normally do not give birth until c. 10 years old (Harcourt & Stewart, 2007).
1st age of breeding for males	13 years	11.5–15.0 years (median 12.8)[1]	13 years reflects data for reintroduced populations, & in mountain gorillas the youngest known father was just under 12 years old (Bradley et al., 2005).
Maximum age of reproduction	39 years		In wild female mountain gorillas age-related patterns in birth rates have been demonstrated, with an apparent decrease from 40 (Robbins et al., 2006). There is evidence for menopause in captive female western gorillas in their 40s (Atsalis & Margulis, 2006).
Sex ratio at birth	50 : 50	70 : 30 (M : F)[1]	Appears to be no published data on sex ratio at birth for wild gorillas, & data from reintroduced populations are based on a small sample size; however, of 114 wild-born orphan western gorillas (all of which were < 4 years of age at time of capture) received at Projet Protection des Gorilles gorilla sanctuaries in Congo & Gabon between June 1989 & December 2008, 57 were male & 57 female (The Aspinall Foundation, unpubl. data).
Annual mortality rate age 0 (1st-year mortality)	25%	18.2% (1st generation)[1]	Published values for 1st-year mortality in wild gorillas vary (8.3 & 42.9% for western gorillas, Robbins et al., 2004; 19.6%, Yamagiwa & Kahekwa, 2001, & 24%, Gerald, 1995, for eastern gorillas). The latter is based on the largest sample size, & we chose a value closest to this for the baseline. Our baseline values for Ages 0, 1 & 2 combined result in a total infant mortality of 33.7%, similar to 34% infant mortality of mountain gorillas (Watts, 1991; Gerald, 1995), & within the range of two wild populations of western gorillas (22 & 65%; Robbins et al., 2004).
Annual mortality rate ages 1 & 2 (2nd & 3rd year annual mortality rate)	6%	0% (1st generation)[1]	See above.
Annual mortality rate ages 3–5 (juvenile annual mortality rate)	2%	1.5% (release stock)[1]	Values used in the baseline scenario for ages 3–11 are slightly higher than those given by King et al. (2012) for the reintroduced populations but give a deterministic total mortality for ages 3–11 of 14%, as in a model developed for mountain gorillas (Robbins & Robbins, 2004; both sexes combined) based on a relatively large data set for these age categories (Gerald, 1995).
Annual mortality rate ages 6–11	1.5%	1.2–1.5% (release stock)[1]	See above.
Annual mortality rate ages 12–17	2.5% (M) 1.7% (F)		Adult mortality data are limited for the reintroduced populations (1.2% annual mortality rate for ages 8–21, after which no data are available; King et al., 2012), so we used the age-dependent sex-specific mortality rates from age 12 used by Robbins & Robbins (2004) for a model developed for mountain gorillas.

			Source
Annual mortality rate ages 18–23	2.2% (M)	1.8% (F)	From Robbins & Robbins (2004; see above).
Annual mortality rate ages 24–29	15.7% (M)	2.9% (F)	From Robbins & Robbins (2004; see above).
Annual mortality rate ages 30–39	10.4% (M)	8.3% (F)	From Robbins & Robbins (2004; see above).
Annual mortality rate ages 40–43	40%		From Robbins & Robbins (2004; see above).
Annual mortality rate age 44	100%		From Robbins & Robbins (2004; see above).
Environmental variability in annual mortality rate	1.5%	1.5%[2]	For the 12-years 1997–2008 the SD in annual mortality rates within reintroduced populations was 3.7%, of which 1.5% could not be accounted for by demographic stochasticity, & could therefore be considered to be because of environmental variability. Sample sizes were too low to calculate environmental variability in mortality rates of different age classes, so 1.5% was used as the input parameter in mortality rates for each age class (including infants).

[1]From King et al., 2012; [2]Calculated in this study

reintroduced populations, using the same dataset analysed by King et al. (2012), notably those relating to environmental variability (EV). This was calculated following Miller & Lacy (2005), using the equation: $s_{EV} = \sqrt{s^2_{EV}} = \sqrt{(s^2_{TOT} - s^2_{DS})}$, where s_{EV} = the standard deviation because of EV, s^2_{EV} = the variance because of EV, s^2_{TOT} = the total variance across the data, and s^2_{DS} = the sampling variance because of demographic stochasticity (DS) = $(p \cdot (1-p))/(x-1)$, where p = the mean annual mortality rate and x = the mean annual initial population size. As reproduction, like mortality, is also binary, we used the same method for calculating environmental variability in annual birth rates. We calculated this for 2003–2008, with one year (2006) excluded as it was an outlier showing an abnormally high birth rate that was clearly a function of the low sample size rather than of environmental variability (four females from a single group gave birth within 2 months of each other, from a total of seven females of breeding age with breeding opportunities within the population at that time).

We defined population extinction as only one sex remaining. Inbreeding depression was included in the baseline scenario using the default values in *Vortex* (3.14 lethal equivalents, with 50% because of lethal alleles). Environmental variation was considered to affect survival and reproduction independently. Reproduction was not considered to be density dependent, and carrying capacity was set at a high level (1,000 individuals per population) to avoid modelling density dependent impacts on population size (although the legally-defined reintroduction sites have a lower carrying capacity, in reality these sites are not isolated from surrounding habitat and we were interested to know the full potential for population growth regardless of legal habitat boundaries). The phenomenon of adult male dispersal from reproductive groups to become solitary and non-reproductive in the longterm (Harcourt & Stewart 2007; King et al., 2012) was simulated in the model by specifying the reproductive system as long-term polygyny, and quantified through the mate monopolization parameter (Table 1).

The two reintroduced populations (in Congo and in Gabon) were modelled separately. The initial population sizes, structures and gene diversities were imported from studbooks for each population, as at April 2009 (excluding one recently born infant from each population whose sex was unknown at the time of the model development). We conducted a sensitivity analysis on the Congo baseline model, to identify the key vital rates requiring better estimates, by investigating the impact on the mean stochastic growth rate of using high and low values for various input parameters. For both populations we simulated the baseline model of no further releases, and five scenarios of varying reinforcement strategies (Table 2). The first reinforcement scenario (R1) modelled the inclusion of the gorillas in the pre-release phase of the programme in each country as at

TABLE 2 Description of modelled scenarios of varying degrees of reinforcement on the baseline populations in Congo and Gabon.

Scenario	Description
R1	Reinforcement with individuals in pre-release phase as at April 2009 (Congo: 2 females & 3 males aged 2–5; Gabon: 3 females & 1 male aged 1–3)
R2	R1 plus 1 group of 3 females & 2 males aged 6 in year 7
R3	R1 plus 2 groups of 3 females & 2 males aged 6 in years 7 & 12
R4	R1 plus 3 groups of 3 females & 2 males aged 6 in years 7, 12 & 17
R5	R1 plus 4 groups of 3 females & 2 males aged 6 in years 7, 12, 17 & 22

April 2009, whereas subsequent reinforcement scenarios modelled hypothetical future releases based approximately on recent rates of arrivals of new gorillas at the rehabilitation centres (King et al., 2005, 2009). A probable scenario of reinforcement of the Congo population was chosen as a baseline for investigating the potential impacts of various catastrophes (Table 3). The first three catastrophe scenarios modelled potential disease outbreaks proposed by primate veterinarians for mountain gorillas *Gorilla berengei berengei* (Miller & Lacy, 2005), and the fourth was intended to model potential outbreaks of an Ebola-like virus. Each scenario was run for 1,000 iterations over 200 years (rather than the more frequently used 100 years because of the relatively long generation time of the species).

The results we recorded for each simulation were deterministic population growth rate (deterministic r), stochastic population growth rate (stochastic r), probability of extinction over the 200 year model period (P(E)), mean number of individuals in surviving populations (extant N), and gene diversity (as a percentage of original diversity), plus standard deviations (SDs) as measures of variability.

Results

Sensitivity testing illustrated that the population model was highly sensitive to changes in the input parameters for annual birth rates, for the number of lethal equivalents, and for female annual mortality rates, especially for adults (Table 4). For example, a value of 0.18 for the annual birth rate rather than 0.20 as in the baseline model reduced the mean stochastic r from 0.004 to −0.003, resulting in an increase in the probability of extinction over 200 years from 9.2 to 29.3%. Conversely, increasing the birth rate to 0.22 resulted in a mean stochastic r of 0.010 and an extinction probability of 2.6%.

The baseline model resulted in a deterministic population growth rate (r) of 0.016. In the baseline scenario of no population supplementation, the mean stochastic population growth rates (r) were $0.004 \pm SD\ 0.053$ and $0.005 \pm SD\ 0.048$ for the Congo and Gabon populations, respectively. Over 200 years this resulted in extinction probabilities of 9.2 and 4.9%, mean extant population sizes of $82 \pm SD\ 73.7$ and $104 \pm SD\ 80.3$, and mean gene diversities of $77.0 \pm SD\ 11.7$ and $80.2 \pm SD\ 10.5\%$ for the Congo and Gabon populations, respectively.

For both populations the model predicted that a single reinforcement with the gorillas in the pre-release phase of the programme in each country as at April 2009 (scenario R1) would have a considerable impact on the viability of the populations compared to the baseline scenario, reducing the probability of extinction over 200 years from 9.2 to 4.0% in Congo, and from 4.9 to 2.2% in Gabon (Table 5). Each subsequent reinforcement scenario modelled also improved viability, with both populations showing a 0% probability of extinction and a mean retention of genetic diversity of > 90% with scenarios R4 and R5 (Table 5).

The four modelled catastrophe scenarios each had major impacts on population persistence (Table 6). Compared to the probability of extinction of 1.8% for the baseline R2 scenario used, the four modelled catastrophe scenarios increased the probability of extinction to between 13.5 and 99%. Gene diversity was also reduced.

Discussion

Population viability analysis

Our primary goal was to evaluate the long-term success of the western lowland gorilla reintroduction programme on the Batéké Plateau. The results from the baseline population viability analysis suggest that the reintroduced gorilla populations have a reasonable chance of persistence (91 and 95% over 200 years, Congo and Gabon populations respectively) but that this probability could be significantly improved by further releases or reinforcements. However, our sensitivity analysis shows that this prediction can be dramatically altered through apparently small modifications of the input parameters to the model, particularly in birth rates, female mortality rates, and inbreeding depression estimates, and also through the inclusion of hypothetical catastrophic events. Some small modifications in demographic input parameters can increase the probability of persistence considerably, as does reducing the impact of inbreeding depression. Conversely, the inclusion of hypothetical catastrophes led to predictions of likely population extinction in all but one scenario.

In addition to population persistence over a specified time-frame, another aspect of population viability is the maintenance of adequate genetic diversity over the course of several generations (Lacy, 1997; Frankham et al., 2002; Goossens et al., 2002; Armstrong & Seddon, 2008). Although some reintroduced populations have been

TABLE 3 Description of modelled scenarios of various catastrophes on the R2 baseline population in Congo (scenarios C1, C2 and C3 were proposed by primate veterinarians for the mountain gorilla *Gorilla berengei berengei*; for more details see Miller & Lacy, 2005).

Scenario	Description	Annual probability of occurrence (%)	Reduction in survivorship	Reduction in reproduction
C1	Influenza-like disease	10	5	0
C2	Severe viral disease	10	25	20
C3	Viral disease with chronic cyclicity	4	25	100
C4	Ebola-like virus	0.5	90	0

TABLE 4 Sensitivity testing of the population model with low and high values of various input parameters, showing their impact on the mean annual stochastic population growth rate r.

Input parameter	Low, Baseline, High*	r range	r difference
Annual birth rate	0.18, 0.20, 0.22	−0.003–0.010	0.013
Lethal equivalents	1.0, 3.14, 5.0	0.000–0.009	0.009
Female annual mortality rate (adult)	B−0.5, B, B+0.5%	0.000–0.008	0.008
Female annual mortality rate (ages 1–9)	B−0.5, B, B+0.5%	0.001–0.006	0.005
Female annual mortality rate (1st year)	22.5, 25, 27.5%	0.002–0.005	0.003
Maximum breeding age	37, 39, 43 years	0.002–0.005	0.003
Mate monopolization	3, 3.5, 7 F : M ratio	0.003–0.004	0.001
Male annual mortality rate (ages 1–12)	B−0.5, B, B+0.5%	0.003–0.004	0.001
Male annual mortality rate (1st year)	22.5, 25, 27.5%	0.004–0.004	0.000
Male annual mortality rate (adult)	B−0.5, B, B+0.5%	0.004–0.004	0.000
Environmental variability in adult female annual mortality rate	B−1, B, B+1%	0.004–0.004	0.000

*B, baseline value

TABLE 5 Summary of results (mean ± SD) of the *Vortex* simulation of several scenarios of varying degrees of reinforcement of the baseline populations in Congo and Gabon over a 200-year period.

	Stochastic r[1]	P(E)[2] (%)	Extant N[3]	Gene diversity (%)
Congo population				
Baseline	0.004 ± 0.053	9.2	83 ± 73.7	77.0 ± 11.69
Scenario R1	0.005 ± 0.047	4.0	109 ± 79.8	81.1 ± 10.92
Scenario R2	0.007 ± 0.043	1.8	150 ± 102.5	85.3 ± 7.33
Scenario R3	0.009 ± 0.041	0.3	194 ± 119.6	88.0 ± 5.56
Scenario R4	0.010 ± 0.039	0.0	248 ± 140.8	90.3 ± 3.90
Scenario R5	0.011 ± 0.039	0.0	288 ± 155.9	91.5 ± 3.12
Gabon population				
Baseline	0.005 ± 0.048	4.9	104 ± 80.3	80.2 ± 10.47
Scenario R1	0.006 ± 0.043	2.2	133 ± 96.2	82.9 ± 8.14
Scenario R2	0.008 ± 0.040	1.0	181 ± 112.3	86.9 ± 6.38
Scenario R3	0.010 ± 0.039	0.2	230 ± 131.2	89.2 ± 4.53
Scenario R4	0.011 ± 0.038	0.0	275 ± 149.3	90.8 ± 3.47
Scenario R5	0.012 ± 0.037	0.0	326 ± 160.3	92.1 ± 2.59

[1]Mean annual population growth rate; [2]Probability of extinction; [3]Mean extant population size

established from < 10 founders (Taylor et al., 2005), and small founder populations do not necessarily lead to severe inbreeding depression (Jamieson et al., 2007), most geneticists consider that a large founder population is necessary to ensure sufficient genetic diversity, to avoid the potentially negative effects of inbreeding depression and to the capacity to adapt to environmental change in the long term (Frankham, 2005; Traill et al., 2010; Groombridge et al., 2012; Jamieson & Lacy, 2012; Keller et al., 2012). Genetic goals in population management often include the retention of 90% of genetic diversity over a specified time period (Frankham et al., 2002).

Based on the current composition of both reintroduced populations the baseline model predicted a retention of c. 80% of genetic diversity over 200 years. The fourth reinforcement scenario (of current reinforcement plans plus

TABLE 6 Summary of results (mean ± SD) of the *Vortex* simulation of scenarios of various catastrophic events on the R2 baseline population in Congo over a 200-year period.

	Stochastic r^1	P(E)[2] (%)	Extant N[3]	Gene diversity (%)
Baseline (R2)	0.007 ± 0.043	1.8	150 ± 102.5	85.3 ± 7.33
Scenario C1	0.000 ± 0.059	13.5	55 ± 46.6	78.0 ± 11.85
Scenario C2	−0.022 ± 0.133	99.0	5 ± 2.0	63.0 ± 13.39
Scenario C3	−0.009 ± 0.103	62.5	26 ± 27.9	69.1 ± 17.31
Scenario C4	−0.002 ± 0.157	47.7	106 ± 103.1	81.0 ± 12.02

[1]Mean annual population growth rate; [2]Probability of extinction; [3]Mean extant population size

three subsequent reinforcements of three females and two males each time) was sufficient in both cases to achieve a 90% retention of genetic diversity. We did not include genetic management, which is used for small captive populations to ensure maximum retention of genetic diversity (Earnhardt et al., 2004), in our model. With the relatively intensive post-release monitoring techniques practised at both sites (King et al., 2012), some level of genetic management may be possible through population manipulation. Given that within gorilla society a few males dominate reproduction, and some fail to reproduce (Harcourt & Stewart, 2007), genetic management in the reintroduced gorilla populations could be effected by manipulating each male's opportunities to breed.

Modelling and reintroduction management

The modelling showed that the populations have the capacity to persist for 200 years, with the probability of persistence and the retained genetic diversity increasing if the populations are gradually reinforced with new individuals over subsequent years. However, the exercise also shows that events beyond the control of management, particularly catastrophes but also factors such as the impacts of inbreeding depression, could jeopardize the populations and lead to their extinctions if they are frequent or severe enough. This conclusion is not unexpected and our results support the current directions in the management of the reintroduction programme, rather than suggesting significant modifications. The quantitative nature of the results does, however, highlight the magnitude of the potential negative impacts of disease-based catastrophes and inbreeding depression, suggesting firstly that reintroduction managers should ensure that pathogen surveillance protocols are regularly updated and applied, and secondly that realistic taxon-specific measurements of inbreeding depression should ideally be more widely available for modelling purposes, given their significant influence for predicting extinction risk (O'Grady et al., 2006).

The continued monitoring of the reintroduced populations will facilitate refinement of the model, particularly for highly sensitive input parameters such as birth rates and female mortality rates, and improve confidence in its predictions and its relevance to decision-making. The model could then provide guidance on issues such as the optimum number of individuals required for reinforcement of the reintroduced populations, and whether genetic management through the manipulation of male opportunities to breed is a strategy worth considering. Integration of such an adjustable model into the decision-making process could, if well structured and defined, lead to an adaptive management approach to reintroduction management (Armstrong et al., 2007; McCarthy et al., 2012).

Monitoring and modelling slow-reproducing long-lived species

In reintroduction programmes for slow-reproducing long-lived species, post-release monitoring needs to be undertaken over a relatively long time-frame, to gather even simple data on post-release survival and reproduction, which can give an indication of the initial success of the programme (King et al., 2012). To assess long-term success an evaluation of population viability is needed, which requires the development of a population model (Armstrong & Reynolds, 2012; Seddon et al., 2012). For long-lived species the collection of the necessary demographic data, particularly mortality rates, could take decades. We were fortunate that our study species has a close relative, the eastern gorilla, one of the best-studied primates (Harcourt & Stewart, 2007; Robbins et al., 2009). We were therefore able to compare our post-release monitoring data with large published datasets for eastern gorillas to verify that our data were realistic and to fill in gaps, particularly concerning adult mortality rates. If such data to develop a realistic population model are not available, reintroduction programmes for other long-lived species would have to wait for sufficient demographic data to be collected either through post-release monitoring or through demographic studies of wild populations.

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Biographical sketches

Tony King plans, implements and evaluates reintroduction and conservation projects, particularly in the Republic of Congo and in Madagascar. He is committed to finding locally-relevant strategies for the conservation of threatened species and their habitats. Christelle Chamberlan has managed conservation projects in the Congo and Madagascar for the past 10 years. She has previously studied elephants and buffaloes in Odzala National Park, Congo, rehabilitated orphan chimpanzees in Congo, and worked with mountain gorillas in Rwanda. Amos Courage has been involved in the gorilla reintroduction programme since the first releases in 1996.