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

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Abstract

The use of population modelling has become an increasingly common tool in reintroduction planning and assessment. Whilst initial reintroduction success is often measured by quantifying post-release survival and reproduction, longer-term reintroduction success is best assessed through measures of the population viability. In this paper we develop a population model capable of providing useful results for influencing reintroduction management decision-making concerning a reintroduction programme of 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 occasionally 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, for 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; demography; Gabon; population model; post-release monitoring; rehabilitation; reintroduction management

Introduction

The use of population modelling is becoming an increasingly common tool in reintroduction planning 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), which is best measured through population viability modelling to investigate the probability of the long-term persistence of a re-established population (Seddon et al., 2007, 2012). Another major

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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 required 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 data used in their development (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 due to low sample sizes (Nichols & Armstrong, 2012). Therefore developing models for long-lived species that provide useful results for guiding reintroduction management decision-making is challenging. Consequently reintroduction programmes of 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 apparently yet to utilise models in planning or assessment. A recent review of the published literature regarding modelling reintroduced populations by 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 due to the geographical bias of publications, with 75 (84%) relating to projects in Europe, North America, New Zealand or Australia, where primates do not occur, and many models are probably not published at all (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 endangered primate.

The western lowland gorilla is classified by IUCN (2012) as Critically Endangered, based on a projected 80% decline in the wild over three generations, the major causes of decline identified as commercial hunting and mortality caused by the Ebola virus (Tutin et al., 2005; IUCN, 2012), with habitat loss and degradation, and possibly climate change, expected to also become major threats (IUCN, 2012). Gorillas can live for over forty years, usually don't reproduce until they are at least 10 years old, and females produce one surviving off-spring only every five years or so (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). With the first releases occurring in 1996 and 2001 in the two countries respectively, post-release monitoring data have recently been analysed to quantify various 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 (King et al., 2012). To assess longer-term success, in this paper we use the demographic data provided for the reintroduced populations by King et al. (2012), in addition to published data on wild and occasionally captive gorilla populations, to develop a population model using the modelling software Vortex. We use the model to investigate how possible scenarios might impact the viability of the two reintroduced populations, and look at how

population models can inform reintroduction management decisions for long-lived species.

Methods

Study populations

The two reintroduced western lowland gorilla populations that are the focus of our study are located in the Lesio-Louna Reserve of Congo and the Batéké Plateau National Park of Gabon. Pre-release preparations and release implementation are described elsewhere (King et al., 2012). The reintroduction sites are the subject of 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). 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-borns (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 release stock aged 8 to 22 years, plus 7 first-generation offspring aged 6 months to 5 years) and 25 in Gabon (16 wild-born and six ex-situ captive-borns aged 7 to 13 years, plus 3 first-generation offspring aged 2 months to 1.5 years). Further releases are expected at both sites (King & Courage, 2008).

Population modelling

We used the freely-available modelling software Vortex (Version 9.94) to develop the population model for the reintroduced gorilla populations. Vortex is appropriate for modelling species with low fecundity and long life-spans (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 populations presented by King et al. (2012), compared with data on wild, or occasionally captive, western and eastern gorillas (Table 1 and references therein). The calculation of a few input parameters required further analysis of the post-release monitoring data from the reintroduced populations, using the same data-set analysed by King et al. (2012), notably those relating to environmental variability (EV). EV in annual mortality rates 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 due to EV, s^2_{EV} = the variance due to EV, s^2_{TOT} = the total variance across the data and s^2_{DS} = the sampling variance due to demographic stochasticity (DS) = $(p * (1 - p)) / (x - 1)$, where p = the mean annual mortality rate and x = the mean annual initial population size. We used the same method for calculating EV in annual birth rates, for the years 2003 to 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 environmental variability).

We defined population extinction as only one sex remaining. Inbreeding depression was included in the base-line scenario using the default values in Vortex (3.14 lethal equivalents, with 50% due to 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 (1000 individuals per population) to avoid modelling density dependant impacts on population size (although the legally-defined reintroduction sites surely 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 long-term (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 monopolisation parameter (Table 1).

The two reintroduced populations (Congo and Gabon) were modelled separately, each as a single population. The initial population sizes, structures and gene diversities were imported from pedigreed studbooks for each population, as at April 2009 (excluding one recently born infant from each population of whom the sex was not known at the time of the model development). We conducted a sensitivity analysis on the Congo base-line 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 base-line 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 April 2009, whilst 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 base-line 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 (Miller & Lacy, 2005), whilst the fourth was intended to model potential outbreaks of the Ebola virus. Each scenario was run for 1000 iterations over a period of 200 years. Two hundred years was used rather than the more frequently used 100 years due to 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 as measures of variability.

Results

Sensitivity testing

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%.

Base-line scenario

The base-line model resulted in a deterministic population growth rate (r) of 0.016. In the base-line scenario of no population supplementation, the mean stochastic population growth rates (r ± standard deviation) were 0.004 ± 0.053 and 0.005 ± 0.048 for the Congo and Gabon populations respectively. Over the 200 year time period, this resulted in extinction probabilities of 9.2 and 4.9%, mean extant population sizes of 82 ± 73.7 and 104 ± 80.3, and mean gene diversities of 77.0 ± 11.7 and 80.2 ± 10.5% for the Congo and Gabon populations respectively.

 Impacts of reinforcements and catastrophes

For both populations, the model predicted that a single reinforcement with the actual groups currently in the pre-release phase at each project would have a considerable impact on the viability of the population compared to the base-line 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 over 90% with scenarios R4 and R5 (Table 5).

The four modelled catastrophes 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 (Table 6).

Discussion

Population viability analysis

Our primary research question was to evaluate the long-term success of the western lowland gorilla reintroduction programme to Batéké Plateau region of central Africa. The results from the base-line model of our 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 can be significantly improved by further releases or reinforcements over the coming years. However, the sensitivity analysis we undertook shows 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 quite considerably, as does reducing the impact of inbreeding depression. Conversely, the inclusion of the 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 generally considered to be 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). While some reintroduced populations have been established from fewer than ten 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 allow the capacity to adapt to environmental change over 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% genetic diversity over a specified time period (Frankham et al., 2002). In both reintroduced populations based on their current composition, the base-line model predicted a retention of approximately 80% genetic diversity over 200 years. The fourth reinforcement scenario (of current reinforcement plans plus three subsequent reinforcements of three females and two males each time) was sufficient in both cases to achieve 90% retention of genetic diversity. It should be noted that we did not include genetic management within our model, which is used within small captive populations throughout the world to ensure maximum retention of genetic diversity (Earnhardt et al., 2004). 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 there is a very unequal distribution between individual male reproductive success, with a few males dominating reproduction, and some failing to reproduce at all (Harcourt & Stewart, 2007), in the reintroduced gorilla populations genetic management could be particularly effective by manipulating each male's opportunities to breed.

Modelling and reintroduction management

The modelling exercise 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 the coming years, but that events outside of the control of the project management team, particularly catastrophes but also factors such as the impacts of inbreeding depression, might jeopardise the populations, and could lead to their extinctions if they are frequent or severe enough. This conclusion is not unexpected, and currently our results support the current directions in the management of the reintroduction programme, rather than suggesting significant modifications. With time, however, the continued monitoring of the reintroduced populations can allow refinement of the model, improving confidence in its predictions and its relevance to decision-making. It 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. Such integration of a modifiable 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 clearly needs to be undertaken over a relatively long time-frame, even to gather simple data on post-release survival and reproduction which can give an indication of the initial success of the programme (King et al., 2012). In order to assess long-term success, an assessment of population viability is required, which

requires the development of a population model (Armstrong & Reynolds, 2012; Seddon et al., 2012). In long-lived species, the collection of the necessary demographic data, particularly concerning mortality rates, from the reintroduced population might take decades. We were fortunate that in our study species, the western gorilla, its close relative the eastern gorilla is one of the best-studied primate species in the world (Harcourt & Stewart, 2007; Robbins et al., 2009). We were therefore able to compare our post-release monitoring data with large published data sets from eastern gorillas to verify that our data were realistic, and to fill in gaps in our data, particularly concerning adult mortality rates. If such data are not available, reintroduction programmes of other long-lived species must either wait for enough demographic data to be collected through post-release monitoring, or must initiate demographic studies of wild populations, if they are to be able to develop a realistic population model.

Acknowledgements

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Biogeographical sketches

Tony King has worked for The Aspinall Foundation for ten years, planning, implementing and evaluating their reintroduction and conservation projects, and has been particularly involved in the Congo and Madagascar country programmes. He also has extensive experience in biodiversity surveys, particularly of insects, birds and bats, and is committed to finding locally-relevant strategies for the conservation of endangered species and their habitats.

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Table 1 Demographic input values used in the base-line model, values for the reintroduced populations based on post-release monitoring results, and rationale behind the choice of each input value. (AMR = Annual Mortality Rate; EV = Environmental Variability; [a] taken from King et al., 2012; [b] calculated during this study)

Parameter	Value used for base-line scenario	Value in reintroduced population	Rationale
Mate monopolisation (% of adult males in breeding pool)	28.6% (= one per 3.5 females)		Studies of five wild populations of western gorillas found the median number of adult females per (predominantly single-male) breeding group to be 3.5 (range of population means 2.9 to 7.1; Harcourt & Stewart, 2007).
Annual birth rate (ABR)	0.20	0.196 [a]	We used a value of 0.20 for annual birth rate in the base-line model, represented as 20% of adult females available to breed each year, with a maximum of one offspring per female per year, similar to the rates given by King et al. (2012) for the reintroduced populations of 0.196, and by Robbins et al. (2004) for two wild populations of western gorillas of 0.198 and 0.180, and for mountain gorillas of 0.226.
EV in ABR	2.4%	2.4% [b]	This value corresponds to the standard deviation of annual birth rates in the reintroduced populations unaccounted for by the expected standard deviation due to demographic stochasticity.
First age of breeding for females	10 years	8.6 to 16.8 years (median 10.3, mean 11.6) [a]	We used ten years as the first age of breeding for females in the base-line population model, as it reflected the data for the reintroduced populations, and because although not measured in wild western gorillas (Robbins et al., 2004), female mountain gorillas, although considered sexually mature from eight years old, normally do not give birth until they are around ten years (Harcourt & Stewart, 2007).
First age of breeding for males	13 years	11.5 to 15.0 years (median 12.8) [a]	We used 13 years as the first age of breeding for males in the base-line population model, as it reflected the data for the reintroduced populations, and because 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 a particularly apparent decrease from the age of 40 (Robbins et al., 2006). There is also evidence for menopause in captive female western gorillas

			in their forties (Atsalis & Margulis, 2006).
Sex-ratio at birth	50:50	70:30 (M:F) [a]	There appears to be no published data on sex-ratio at birth for wild gorillas, and the data from the reintroduced populations are based on a small sample size; however, of 114 wild-born orphan western gorillas received at the PPG gorilla sanctuaries in Congo and Gabon between June 1989 and December 2008, all of which were less than four years of age at the time of capture and can be assumed to represent a random sample of infants in the wild population, 57 were males and 57 were females (The Aspinall Foundation, unpubl. data).
AMR Age 0 (First-year mortality)	25%	18.2% (first generation) [a]	Published values for first-year mortality in wild gorillas vary considerably, with figures including 8.3% and 42.9% for western gorillas (Robbins et al. 2004), and 19.6% and 24% for eastern gorillas (Yamagiwa & Kahekwa 2001 and Gerald 1995 respectively). The last of these is based on the largest sample size, hence why we chose a value closest to this for our base-line scenario. Additionally, our base-line values for Ages 0, 1 & 2 combined result in a total infant mortality of 33.7%, similar to the 34% infant mortality given for mountain gorillas (Watts, 1991; Gerald, 1995), and within the range given for two wild populations of western gorillas of 22% and 65% (Robbins et al., 2004).
AMR Ages 1 & 2 (Second and third year annual mortality rate)	6%	0% (first generation) [a]	See above
AMR Ages 3, 4 & 5 (Juvenile annual mortality rate)	2%	1.5% (release stock) [a]	The mortality figures we used in the base-line scenario for ages 3 to 11 are slightly higher than those given by King et al. (2012) for the reintroduced populations, but give a deterministic total mortality from age 3 through 11 of 14%, as in a model developed for mountain gorillas by Robbins & Robbins (2004; both sexes combined) based on a relatively large data-set for these age categories given by Gerald (1995).
AMR Ages 6 to 11	1.5%	1.2 to 1.5% (release stock) [a]	See above
AMR Ages 12 to 17	2.5% (M) 1.7% (F)		Adult mortality data are limited for the reintroduced populations (1.2% AMR from age 8 to 21, after which no data is available; King et al., 2012), so we used the age-dependant sex-specific mortality rates from age 12 used by Robbins & Robbins

			(2004) for their model developed for mountain gorillas
AMR Ages 18 to 23	2.2% (M) 1.8% (F)		From Robbins & Robbins (2004; see above)
AMR Ages 24 to 29	15.7% (M) 2.9% (F)		From Robbins & Robbins (2004; see above)
AMR Ages 30 to 39	10.4% (M) 8.3% (F)		From Robbins & Robbins (2004; see above)
AMR Ages 40 to 43	40%		From Robbins & Robbins (2004; see above)
AMR Age 44	100%		From Robbins & Robbins (2004; see above)
EV in AMR	1.5%	1.5% [b]	For the 12-year period 1997 to 2008, the standard deviation in annual mortality rates within the reintroduced populations was 3.7%, of which 1.5% could not be accounted for by demographic stochasticy, and could therefore be considered as due to environmental variability (EV). Sample sizes were too low to calculate EV in mortality rates of different age-classes, so 1.5% was used as the input parameter for EV in mortality rates for each age-class (including infants) in the population model.

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

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

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6 Table 3 Description of modelled scenarios of various catastrophes on the R2 baseline
7 population in Congo.

	Annual probability of occurrence	Reduction in survivorship	Reduction in reproduction
Scenario C1	10%	5%	0%
Scenario C2	10%	25%	20%
Scenario C3	4%	25%	100%
Scenario C4	0.5%	90%	0%

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11 Table 4 Sensitivity testing of the population model with low and high values of
12 various input parameters, showing their impact on the mean annual stochastic
13 population growth rate r (B = baseline value; AMR = annual mortality rate; EV =
14 environmental variability).

Input parameter	Low, Baseline, High	r range	r difference
Annual birth rate	0.18, 0.20, 0.22	-0.003 to 0.010	0.013
Lethal equivalents	1.0, 3.14, 5.0	0.000 to 0.009	0.009
Female AMR (adult)	B-0.5, B, B+0.5 %	0.000 to 0.008	0.008
Female AMR (ages 1 to 9)	B-0.5, B, B+0.5 %	0.001 to 0.006	0.005
Female AMR (first year)	22.5, 25, 27.5 %	0.002 to 0.005	0.003
Maximum breeding age	37, 39, 43 years	0.002 to 0.005	0.003
Mate monopolisation	3, 3.5, 7 f:m ratio	0.003 to 0.004	0.001
Male AMR (ages 1 to 12)	B-0.5, B, B+0.5 %	0.003 to 0.004	0.001
Male AMR (first year)	22.5, 25, 27.5 %	0.004 to 0.004	0.000
Male AMR (adult)	B-0.5, B, B+0.5 %	0.004 to 0.004	0.000
EV in adult female AMR	B-1, B, B+1 %	0.004 to 0.004	0.000

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17 Table 5 Summary of results (mean ± SD) of the Vortex simulation of several
18 scenarios of varying degrees of reinforcement of the base-line populations in Congo
19 and Gabon over a 200 year period (where r = mean annual population growth rate,
20 P(E) = probability of extinction, and Extant N = mean extant population size).

	Stochastic r	P(E) (%)	Extant N	Gene diversity (%)
Congo population				
Base-line	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				
Base-line	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

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24 Table 6 Summary of results (mean ± SD) of the Vortex simulation of scenarios of
25 various catastrophic events on the R2 base-line population in Congo over a 200 year
26 period (where r = mean annual population growth rate, P(E) = probability of
27 extinction, and Extant N = mean extant population size).

	Stochastic r	P(E) (%)	Extant N	Gene diversity (%)
Congo population				
Base-line (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

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