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Giraffe Translocation Population Viability Analysis

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ABSTRACT Guidelines for translocations recommend that population modelling should be

used in translocation projects to assist in the assessment of project feasibility. We simulated

various scenarios of translocated giraffe populations to identify viable age and sex distributions

of founding populations using Population Viability Analysis implemented in Vortex software.

KEYWORDS founding population, giraffe, population model, PVA, translocation, population

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Guidelines for translocations suggest population modelling should be used to assist in the

assessment of project feasibility (IUCN 2013). Population modelling for translocation projects

can provide estimates of population persistence, assess longer-term viability, explore the possible

short-term consequences of management strategies, identify key vital rates (Seddon et al. 2007),

and offer guidance on age- and sex-classes for founder populations. Population viability analysis

(PVA) is commonly used to predict the likely future status of a population and thus provides a

quantitative basis for evaluating alternative management strategies (Boyce 1992, Morris and

Doak 2002). The availability of commercial software programs such as Vortex has facilitated the

application of population modelling in reintroduction planning (e.g., Bustamante 1998) and post-

release evaluation (e.g., Slotta-Bachmayret et al. 2004).

Giraffes (*Giraffa camelopardalis*) are endemic African ruminant ungulates, and one of only a

handful of extant terrestrial megaherbivores (Owen-Smith 1988). Most populations of giraffes

have declined in recent decades, leading to the recent decision to upgrade the species to

vulnerable status on the IUCN Red List (Muller et al. 2018). Translocations have been used as

conservation tools to re-introduce giraffes to previously occupied areas or establish new

populations (Winter et al. 2019). We simulated various scenarios of translocated giraffe

populations to identify the optimal age and sex distribution of a founding population using PVA

implemented in Vortex software (Lacy and Pollack 2017). We used stochastic, single-population,

individual-based models to project future population trajectories and estimate probability of

persistence, population growth rate, and genetic diversity at a hypothetically ideal prospective

release sites under different founder population release scenarios. Scenarios varied the numbers

of females and males to release (Converse et al. 2013) and considered 3 population models with

demographic rates simulating slow, moderate, and fast population growth rates.

METHODS

PVA Scenarios

We constructed population models in program Vortex to simulate a hypothetical translocated

population where both males and females bred from ages 5 to 25, the maximum age of survival

for both sexes was 25 years, females always produced 1 calf, and sex ratio at birth was equal

(Dagg 2014). Within the model parameters, offspring were dependent upon their mother for 1

year, meaning that if the mother died during the calf's first year, then the calf also died (Dagg

2014). All males aged 5 and above were in the breeding pool. Demographic rates are given in

Table 1.

Table 1. Demographic rates used to parameterize population simulations.

Population growth	Slow		Moderate		Fast	
Lambda	1.001		1.010		1.024	
Demographic rates	%	(SD)	%	(SD)	%	(SD)
Mortality Age 0-1	50	(10)	50	(10)	40	(10)
Mortality Age 1-2	20	(6)	20	(6)	20	(6)
Mortality Age >2	5	(3)	5	(3)	5	(3)
Reproduction	45	(10)	50	(10)	50	(10)

61 To parameterize our PVA, we based our demographic rates on published observations of means

62 and variances of age-specific survival and fecundity for wild giraffe populations throughout

63 Africa (Lee and Strauss 2016), and data for reproductive longevity and inbreeding depression

64 from captive animals (Lackey 2009). We used data from IUCN Red List assessments to compute

65 mean population growth rates for seven growing giraffe subpopulations, including some

66 translocations (Muller et al. 2018). Mean observed population growth rate was 1.024 (range

67 1.0045 to 1.035). Because the highest observed growth rates were from short time spans, they

68 were likely due to transient population dynamics and not the asymptotic growth rate. Therefore,

69 in our PVA we simulated populations with 3 different demographic parameterizations with

70 different asymptotic population growth rates that represented slow- (1.001), moderate- (1.010),

71 and fast-growing (1.024) populations. The fastest population growth rate is probably only

72 achievable in translocation destinations that have few or no large predators.

73 Given that few individuals typically are translocated on any given occasion, demographic

74 stochasticity, Allee effects, and inbreeding depression could all adversely affect probability of

75 persistence for translocated populations (O'Grady et al. 2006; Deredec and Courchamp 2007;

76 Van Houtan et al. 2010). We chose to include stochasticity (demographic rates vary among

77 individuals and over time) and inbreeding depression (reduced reproduction and calf survival due

78 to inbreeding) in our simulations because these effects are likely to exist in giraffe populations

79 (O'Grady et al. 2006, Lackey 2009, Lee and Strauss 2016, Lacy and Pollack 2017). We did not

80 include Allee effects (reduced demographic rates at small population size) because Allee effects

81 are unlikely in giraffe populations, especially in enclosed reserves. We set demographic temporal

82 correlation between mortality and reproduction due to environmental variation at 0.5. We

83 included inbreeding depression using Vortex values representing a genetic load of 6.29 total

84 lethal equivalents per individual, of which 50% are due to recessive lethal alleles, and the

85 remainder are lethal equivalents not subjected to removal by selection (O'Grady et al. 2006,

86 Lacy and Pollack 2017). We assumed zero translocation-related mortality. If mortality is

expected during the translocation process, the simulation results should be interpreted assuming

the actual number of successful live releases. We assumed zero post-release dispersal

movements because many translocations will likely be into fenced or otherwise constrained

areas, and because in our model we wanted to keep track of every individual in the translocated

population.

We projected 50 PVA scenarios. We simulated 50 different populations with various numbers of

2-year-old females released (1, 2, 3, 4, 5, 6, 7, 10, 20, and 40 females) and different numbers of

2-year-old males released to vary the sex ratio (SR) at release (SR = males / females, range =

0.03 to 1.00).

For all scenarios we ran 10,000 iterations of our stochastic model to project the populations for

50 years. We selected a projection time of 50 years because giraffes are a long-lived species and

we were most interested in the longer-term implications of translocation decisions, particularly

the effect of the number of individuals released. Extinction definition was $N < 2$. We assumed a

hypothetically ideal release site, so we did not include effects of density dependence or carrying

capacity. This was done because we were primarily interested in the effects of demography and

genetics without the confounding effects of habitat limitation, which varies considerably between

translocation sites. Forage quality and availability and carrying capacity at the release site should

be quantified as part of a comprehensive pre-translocation assessment. For each scenario, we

recorded output on mean population size in each year, probability of extinction, and gene

diversity in the final extant population.

RESULTS

Females with the greatest reproductive value in our population model were those aged 5 and 6,

with an expected lifetime reproduction of 3.6 and 3.5 females per individual, respectively.

Population projections from all our scenarios followed the same general post-release trajectory

(**Fig. 1**). Overall, there was an initial population decline for 3 years as some released individuals

died before maturity, followed by 22 years of rapid population growth as the founders and their

offspring reproduced, then a steep decline in year 23 as the remaining founding animals died.

This was followed by a brief 3-year period of stable or positive growth until the first post-

founder generation died and stable age distribution was achieved (**Fig. 1**). Scenarios only showed

long-term (50-year) viability (<0.01 probability of extinction) if 40 females and >2 males were

released, regardless of the underlying asymptotic growth rate. The 50-year probability of

extinction declined as the number of released females, and sex ratio, increased (**Fig. 2**). The 50-

year probability of extinction did not fall below 0.10 until release included >10 females and >1

male. Final gene diversity (expected heterozygosity) increased with larger numbers of females

and males in the founding population (**Fig. 3**).

Figure 1. Mean population trajectories from 10,000 iterations of 50-year stochastic population projections of 50 simulated populations of translocated giraffes with varying numbers of females and males. All projections were based on 2-year-old giraffes translocated into suitable habitat with identical demographic parameters (asymptotic population growth rate = 1.01), and included effects of inbreeding depression.

Figure 2. 50-year probability of extinction decreased as the number of released females

increased in population projections simulating translocations of differing numbers of wild

giraffes where asymptotic population growth rate was 1.01 and the effects of inbreeding

depression were included.

Figure 3. Gene diversity in final extant populations increased as the number of released females

increased in 50-year population projections simulating 50 translocations of wild giraffes. Results

are from program Vortex simulations of giraffe translocations.

DISCUSSION

The ideal female age class for translocations in terms of population growth rate is 5 years old,

because this age class immediately begins reproducing, but adults of this age are logistically

challenging to move due to their large body size. All of our population projections used the

logistically more tractable age class of 2-year-olds for translocation, as this age class is often

chosen for translocations. Translocating juveniles means there is an inevitable initial post-release

decline in population size as animals are subject to mortality before reaching reproductive age

(**Fig. 1**). Population projections from all our scenarios followed the same general post-release

trajectory (**Fig. 1**). This pattern is partly the consequence of our specific population model

structure, but it is still extremely informative regarding the effects on population viability and

genetic diversity from different numbers and sex ratios of animals released into the translocated

population. Particularly informative was the significant negative effect that inbreeding

depression can have on long-term population viability.

During the "founders' years" from year 4 to 23, initial population growth will likely be positive

if 2 or more females are translocated (**Fig. 1**). However, this initial growth is a transient effect of

the young-skewed age distribution of the founding population, and very few translocations of

small founding populations will be viable in the long term (**Fig 2**). Increasing the number of

females in the initial release had a strong positive effect on mean annual population growth rate,

and the optimal sex ratio decreased as number of females increased meaning that fewer males

need to be translocated. Maximum observed mean annual growth rate during the founders' years

was realized with a release of 40 females and 4 males.

Following the founders' years, our simulations indicated a slowing of observed growth in all

populations due to the population reaching a stable age distribution of young and old animals and

inbreeding depression reducing fecundity and first-year survival of calves. A negligible

probability of extinction was achieved if the founder population included 40 females and >2

males. In situations where the translocation destination has few or no large predators, and

asymptotic growth rates could approach 1.024, then viable populations could be achieved with

releases of a minimum of 20 females and 4 males.

Future research to inform translocation PVA analyses should focus on quantifying inbreeding

depression in wild or semi-wild populations that have experienced a population bottleneck, and

determining whether Allee effects are present in small populations of wild giraffes. Published

accounts of translocation outcomes including annual population growth rates are also needed as

giraffe translocations are typically not documented (Winter et al. 2019).

MANAGEMENT IMPLICATIONS

Most translocations of fewer than 40 female giraffes will likely not result in long-term viable

populations. Transient population dynamics will result in initial population growth in almost all

cases that in the short term appear to indicate a successful translocation. Rules of thumb for

translocations such as we presented here should not be used as a substitute for project-specific

monitoring and analyses, but they can be useful in early decision-making and feasibility

analyses.

Ideally, every translocation should be conducted under an adaptive management framework with

continuous pre- and post-translocation monitoring of the source and destination populations and

annual updates to PVA analyses to inform structured decision-making. The use of continuous

monitoring, formal and transparent decision-making, and data-driven adaptive management

cycles will generate the necessary data to estimate demographic parameters, identify prospective

subject animals, predict population viability, and make informed management decisions.

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