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Population viability analysis of the population of Raffles' banded langurs *Presbytis femoralis* in Singapore

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Abstract. Population viability analyses (PVAs) have become a useful tool in wildlife conservation because of their ability to assess the relative impact of threats on populations and identify the most effective management scenarios for endangered species. The Raffles' banded langur (*Presbytis femoralis*) is classified as Critically Endangered, with populations occurring in Peninsular Malaysia and the island of Singapore. In Singapore, as of 2021, 68 individuals remain, up from approximately 40 in 2010. A key goal listed in a recent species action plan was to increase the population size. In this study, a PVA was conducted to model the integrated effects of deterministic and stochastic factors on estimated growth trajectories. VORTEX software was used to model the relative impact of threats (habitat loss and low genetic diversity) and management scenarios (increased habitat connectivity, translocation of conspecifics from Malaysia) on population growth rates within a 50-year period. Our modelled results estimated the probability of extinction to be 0% in every scenario and the baseline predicted a population of 244 individuals by 2071 with current population growth rates. The impacts of inbreeding on the population were low, with minimal variation from the baseline scenario. The primary constraint to future population growth is habitat availability, with the population having the potential to reach carrying capacity within the next 40–50 years even if improved habitat connectivity allows increased access to neighbouring forest fragments. With this study, we provide further support for the top management priorities of habitat protection and connectivity identified in the species action plan. There is an urgent need to identify other suitable habitats for the species within Singapore to support future population expansion towards numbers consistent with long-term demographic and genetic viability, with the positive impact of translocations likely to be minimal unless carrying capacity can be increased. With populations of most primate species decreasing and cities playing an increasingly crucial role as a refuge for remaining wildlife populations, this study also demonstrates the potential for populations to recover with effective management, with population growth in the Singapore Raffles' banded langur population demonstrated in all threat scenarios modelled. Conservationists can utilise the strategies employed in Singapore to safeguard similar primate populations in fragmented habitats.

Key words. carrying capacity, habitat loss, langur, population modelling, Singapore, VORTEX

INTRODUCTION

Southeast Asia is home to several biodiversity hotspots (Mittermeier et al., 2011) but also contains the highest proportion of threatened mammal species (Sodhi et al., 2010; Francis, 2019). This is primarily due to rising human populations driving substantial and increasing levels of deforestation within the region (Sodhi et al., 2010). Primates face a particularly high level of threat, with 89% of the Southeast Asian primates listed as threatened (IUCN, 2020), against ~60% globally (Estrada et al., 2017). The primary threat to primates within Southeast Asia is the loss of habitat for conversion to agriculture, closely followed by hunting and trade (Boonratana, 2013; Estrada et al., 2017, 2018; Hughes, 2017; Estoque et al., 2019).

Population viability analyses (hereafter 'PVAs') have become a key conservation tool since their initial development in the 1980s (Frankham et al., 2010). These analyses use models to determine the interactive and cumulative effects of stochastic (chance) and deterministic (known) factors on populations and identify factors which may make them more vulnerable to extinction. The primary use of a PVA is an assessment of the relative impact of threats and management strategies on populations to enable the formulation of evidence-based conservation strategies (Lindenmayer et al., 1993; Frankham et al., 2010; Lacy, 2019; Lacy et al., 2021). Although population viability was previously defined in terms of the probability of extinction, the goal of a PVA will depend upon conservation goals for the species being studied; for one, viability may mean a certain number of individuals, or for another, a certain population growth rate (Lacy, 2019).

As with all modelling, the reliability of the outcomes of a PVA depends on the quality of the data available to run the models. For a PVA, this includes life history data,

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information on population sizes, and realistic data on threats and opportunities for conservation at present and in the near future. As one of the best-studied taxonomic groups globally, primates are excellent models to test the applicability of PVAs. As such, PVAs have been used to inform conservation management in several primate species with practical recommendations including regular supplementation in a reintroduction program for western lowland gorillas (*Gorilla gorilla gorilla*) in Central Africa (King et al., 2014); documentation of the most suitable populations from which to supplement individuals within Cat Ba langur (*Trachypithecus poliocephalus*) groups in Vietnam (Lees et al., 2014); identification of key risk factors for yellow fever outbreaks in brown howler monkeys (*Alouatta guariba clamitans*) in Argentina (Moreno et al., 2015); guidelines on minimum sizes of habitat fragments needed in yellow-breasted capuchin monkeys (*Sapajus xanthosternos*) in Brazil (Da Silva et al., 2016); and a need for improved forest patrols and awareness campaigns to reduce the effects of hunting and deforestation in Javan gibbons (*Hylobates moloch*) (Smith et al., 2017).

Raffles' banded langur (*Presbytis femoralis*) is one of 19 species of *Presbytis* langurs that are distributed from southern Thailand and Myanmar in the north, Java in the south, and Borneo in the east (Matsuda et al., 2022). *Presbytis femoralis* was formerly recognised as a species with three subspecies: *P. f. femoralis*, *P. f. percura*, and *P. f. robinsoni* (Groves, 2001). A recent genetic study, however, has revealed that each is a distinct species (Ang et al., 2020), with the nominate form, the Raffles' banded langur (*P. femoralis*) occurring in Peninsular Malaysia and Singapore. The species is assessed as Critically Endangered based on a small population size and decline (Ang et al., 2021a), and is considered one of the top 25 most endangered primates in the world (Ang et al., 2022). Raffles' banded langurs usually form social groups of one adult male alongside several adult females and their offspring, with a generation length of 10–12 years (Ang et al., 2021a). The species is arboreal, descending to the ground primarily to feed on food (e.g., fallen fruits) or when required to do so to move between forest fragments (Ang & Jabbar, 2020).

Pitra et al. (1995) first conducted a PVA for the Raffles' banded langur population in Singapore after the loss of habitat led to severe bottlenecks in the 1970s and 1980s, with estimates of only 10–14 individuals remaining in 1990 (Hüttche, 1994; Pitra et al., 1995). In that PVA, it was estimated that the population was likely to go extinct within the next 40 years (i.e., by around 2035) based on a small population size and an estimated habitat carrying capacity of just 60 individuals, with recommendations for translocations of 24 individuals from Malaysia needed to maintain viability, i.e. a supplementation of a group of six individuals (two subadult males and four subadult females) every 10 years for 40 years (Pitra et al., 1995). A species action plan from a workshop in 2016 also highlighted the translocation of individuals from Malaysia to Singapore as a potential management strategy to restore gene flow and increase genetic diversity (Ang et al., 2016). The species action plan identified current primary threats to the population as loss, fragmentation, and degradation of habitat resulting from urban development, low genetic variability, and incidences of roadkill resulting from a lack of arboreal connectivity between forest fragments (Ang et al., 2016). Hunting and poaching were not listed as threats to this species in Malaysia and Singapore (Ang et al., 2016; Ang et al., 2021a). The number one management priority identified in addition to supplementation was to protect current habitats and establish corridors to reconnect forest fragments (Ang et al., 2016).

Now, 25 years into the 40-year period that was used in the PVA by Pitra et al. (1995) and with a species action plan recently produced for the population, it is timely to assess the relative impact of each threat identified on population growth before comparing the potential effectiveness of two suggested management scenarios: improved connectivity between forest fragments and translocation of individuals from Malaysia. Our findings will be used to inform upon which threats pose the highest risks to the Raffles' banded langur population in Singapore and to prioritise the most effective management scenarios to ensure the future growth of this population.

MATERIAL AND METHODS

At present, the population of Raffles' banded langur in Singapore is among the best studied langur populations and one of the few for which regular complete population assessments have been made. A study between 2008 and 2010 estimated that the Singapore population of Raffles' banded langurs was 40 individuals, with at least six infants born during that period (Ang et al., 2010). An analysis of their mitochondrial DNA demonstrated that the Singapore population exhibited extremely low genetic variability (Ang et al., 2012; Srivathsan et al., 2016). In 2021, the population size of the langurs in Singapore was 68 individuals in 11 groups, with an average group size of six (range 1–13). The sex ratio of known individuals was approximately 50:50 with 26 females and 24 males (18 unknown) (Ang & Jabbar, 2022).

Study site. The range of current and potential habitat for Raffles' banded langurs within Singapore is shown in Table 1. Here, current habitat refers to areas where these langurs are currently found, while potential habitat refers to adjacent areas where they have not been documented to occur or have previously gone extinct.

Raffles' banded langurs previously inhabited Bukit Timah Nature Reserve (BTNR) but were extirpated from this area after the Bukit Timah Expressway (BKE) was built in the 1980s which fragmented a once continuous habitat (Ang et al., 2016; Chan & Davison, 2019). In 2013, an eco-link bridge was established to reconnect the Central Catchment Nature Reserve (CCNR) and BTNR (Chan & Davison, 2019). An incidence of roadkill in 2017 on the BKE (Ang & Jabbar, 2020) (Fig. 1) suggests that the langurs do attempt to access BTNR and that it constitutes a potential habitat. In 2021,

Table 1. Current and potential habitats for the Raffles' banded langurs in Singapore, and the corresponding area in km^2 (Source of areas for habitats: NParks, 2021)

Habitat type	Habitat	Area in km^2	Total in km^2
Current	Central Catchment Nature Reserve	4.55	8.7
	Chestnut Nature Park	0.81	
	Dairy Farm Nature Park	0.63	
	Lower Peirce Reservoir Park	0.10	
	MacRitchie Reservoir Park	0.12	
	Forested land under military use	1.00*	
	Thomson Nature Park	0.51	
	Upper Peirce Reservoir Park	0.04	
	Upper Seletar Reservoir Park	0.15	
	Windsor Nature Park	0.75	
Potential	Bukit Timah Nature Reserve	1.63	2.7
	Hindhede Nature Park	0.09	
	Rifle Range Nature Park	0.67	
	Springleaf Nature Park	0.18	
	Zhenghua Nature Park	0.17	

*Area estimated using Google Maps. This forest lies to the east of the CCNR.

one langur was observed in Dairy Farm Nature Park (Khoo et al., 2021), which is adjacent to BTNR.

Modelling and definitions. We used VORTEX V.10.5.5 (Lacy & Pollak, 2021) to model the Raffles' banded langur population and for all analyses due to its suitability for modelling small populations of mammalian species with low fecundity and long lifespans (Lacy, 1993). The model works on an individual basis by simulating events including reproduction, mortality, and supplementation until the population reaches a carrying capacity set by the user. It is recommended that at least 500 iterations are selected, with each iteration integrating deterministic processes with demographic, genetic, and environmental stochastic events. This results in multiple slightly varied outputs reflecting the range of possibilities for a population, which the program summarises as mean values across all simulations (Lacy et al., 2021).

The model is first run to assess the deterministic probability of population persistence within the limitations and assumptions of the input data before sensitivity testing is carried out across a range of plausible values to assess the impact of potential threats. The probability of population persistence under varying management scenarios can then be assessed (Frankham et al., 2010; Lacy, 2019; Lacy et al., 2021). To assess the strength of the baseline model for the Raffles' banded langur population, a retrospective analysis was conducted to determine its ability to predict growth from an estimated number of 40 individuals in 2010 (Ang, 2010) and 10–14 individuals in 1990 in the previous PVA (Pitra et al., 1995).

With the species action plan for Raffles' banded langurs stating population growth and genetic viability as key goals (Ang et al., 2016), mean population size (N-extant) and mean genetic diversity (the percentage of genetic diversity retained from the original population) were categories of focus. Additional data were recorded on the probability of extinction (PE), deterministic growth rate (det-r), and mean stochastic growth rate (stoch-r) with measures of variability across iterations included as standard deviations (SD) for each value (Lacy et al., 2021). Years taken to reach carrying capacity were recorded as the year in which the population reached the final mean number of extant individuals, retrieved from yearly output summaries for scenarios. Extinction was defined as when only one sex remained (Lacy et al., 2021). The model was run for a 50-year period, with this deemed to be a suitable time frame for management recommendations to be formulated and implemented.

Limited life history data is a common issue for many species but not a reason to delay a PVA (Frankham et al., 2010; Lacy, 2019), with information from other closely related species used in cases where recent estimates are not available (Frankham et al., 2010). Parameter values used in the model are shown in Table 2 with data available from wild populations of the most closely related species used where data was lacking for our study species (Yeager & Kirkpatrick, 1998; Van Hooff et al., 2005; Wich et al., 2007; Ehlers Smith et al., 2013; Hanya & Bernard, 2016).

Catastrophes were not included as natural disasters are rare in Singapore (AHA, 2015). The group of 68 langurs were modelled as one population based on a shared core habitat so dispersal rates were not included. It was assumed that all males had equal access to females, with mate monopolisation set to 100%.

Mortality rates for this population are thought to be lower than in other similar species due to the absence of threats from poaching and hunting. Mortality resulting from natural predation was set at zero as large predators are either extinct (e.g., tigers (*Panthera tigris*), leopards (*P. pardus*), clouded leopards (*Neofelis nebulosa*)) or very rare within the area where the langurs occur (e.g., changeable hawk-eagles *Nisaetus cirrhatus*)) (Corlett, 1992; Fam & Nijman, 2011; Lim, 2019). There was tracking of 11 Raffles' banded langurs groups ranging from sizes 1 to 13 from 2017 to 2021 (Ang & Jabbar, unpublished) and two mortalities, both from roadkill (one subadult male in 2017 and one juvenile male in 2021) were observed within this tracking period (Ang & Jabbar, 2022). VORTEX assigns annual percentage mortality by age-sex classes. Without known age-sex class breakdowns for this population, we used stable age distributions of age-sex classes assigned in VORTEX as a best estimate for the number of juvenile (aged 1–2) and sub-adult (aged 4–5) males, which resulted in respective mortality rates of 7% and 10% (see Table 2). We assigned a mortality rate of zero for all other age-sex classes. This approach is similar to a PVA conducted on the cao vit gibbon (*Nomascus nasutus*), another Critically Endangered primate inhabiting protected areas with some human presence but no known incidences of hunting (Fan et al., 2013). Fan et al., (2013) monitored three out of 18 cao vit gibbon groups over five years and observed instances of mortality in infants aged 0-1 and juveniles aged 3-4 only, assigning mortality rates of zero to other age-sex classes.

Carrying capacity was calculated by dividing available habitat by the estimated group home range and multiplying by average group sizes of six.

Sensitivity testing of threats. The primary threat outlined within the species action plan was the loss of habitat, with 1 km^2 of habitat currently not designated as nature reserve or nature park (i.e., military land; see Table 1). Loss of this habitat would result in a reduction in carrying capacity of approximately 29 individuals, resulting in a scenario in which the maximum carrying capacity of the population is reduced from 247 to 218.

Recent evaluations of mitochondrial DNA diversity within the Raffles' banded langurs population in Singapore were indicative of extremely low genetic diversity (Ang et al., 2012; Srivathsan et al., 2016). The population is likely to have suffered from inbreeding, which can increase the likelihood of extinction (Frankham et al., 2010; Ang et al., 2012; Ang et al., 2016). This can be modelled in VORTEX through the addition of 'lethal equivalents', which is a measure of sensitivity to inbreeding depression (Lacy et al., 2021). The default setting is for 6.29 lethal equivalents (50% due to lethal alleles) but some argue that 12 are needed to realistically model the impact of inbreeding in wild populations (O'Grady et al., 2006; Lacy et al., 2021). Without accurate estimates for the Raffles' banded langurs, both values are included here to assess the sensitivity of the model to 'low' and 'high' levels of inbreeding depression. Inbreeding depression was not included in the baseline model to compare results with and without inbreeding depression and document any potential impacts this may have on population viability (Lacy et al., 2021).

Management scenarios. Researchers have recommended increased opportunities for connectivity between CCNR and BTNR after a range of species have been documented to be using the eco-link bridge built in 2013 (Chan & Davison, 2019). Improved connectivity between these nature reserves and other adjacent forest patches would result in an increase in accessible habitat area from 8.7 km^2 to 11.4 km^2 and subsequently an increased carrying capacity from 247 to 325 individuals.

Supplementing the population was recommended in the previous PVA and the 2016 species action plan as a measure to increase genetic diversity (Pitra et al., 1995; Ang et al., 2016). With conflicting ideas surrounding the required number of individuals needed to increase genetic diversity in small populations (Frankham et al., 2010) the impact of supplementing one adult male will be compared to the impact of supplementing with a group of one adult male, four adult females and one infant female. Supplementations in VORTEX can be set to yearly intervals within a defined time period, with two supplementations over a 10–year period chosen as a practical goal from a population management perspective.

A final model will evaluate the combined impact of the two management scenarios predicted to have the greatest impact: improved habitat connectivity and group supplementation. Table 3 shows a summary of parameters used for threats and management scenarios.

RESULTS

Baseline model and retrospective analysis. Our baseline model predicted a mean number of 245 individuals extant by 2071 with a mean retention of 98.0% of initial genetic diversity. With no threats included in the baseline scenario, the deterministic growth rate (0.050) and the mean stochastic growth rate (0.049) did not markedly differ and there was 0% probability of extinction (Table 3). The retrospective analysis found that the baseline model was able to effectively predict population growth trajectories that encompassed current population estimates based on the most accurate population estimates from 2010, with a starting population of 40 individuals resulting in a mean population of 69 ± 12 individuals within an 11–year period (Fig. 1). The retrospective analysis from the previous PVA population estimate from 1990 also resulted in population growth trajectories encompassing current population estimates, with the lower starting population estimate of 10 individuals in 1990 resulting in a mean population of 47 ± 24 individuals, and the upper starting population estimate of 14 individuals in 1990 resulting in a mean population of 65 ± 27 individuals within a 31-year period (Fig. 1).

Sensitivity testing of threats. Low and high levels of inbreeding reduced the mean rate of stochastic population growth by 6–8% (change in r = 0.003–0.004) from the baseline model. The impact of this on the mean number of extant individuals resulting was minimal, even for high levels of inbreeding (Table 2; Fig. 1). Loss of forested land

Table 2. Vortex parameters, input values and rationale for the baseline scenario for the Raffles' banded langur population in Singapore (EV, environmental variance; SD, standard deviation).

Vortex parameter	Value	Rationale
Number in population, age and sex breakdown	68	Population size from most recent survey data (A. Ang unpublished data, 2021). As age-sex classes were unknown for all groups, a stable age distribution was selected.
Sex ratio at birth	Equal	Ratios are approximately 50% for known individuals within the population (A. Ang, unpublished data, 2021).
EV correlation between reproduction and survival	1	It can be assumed that good years for reproduction will also be good years for survival in non-migratory species (Lees et al., 2014).
Reproductive system	Polygynous (short term)	Raffles' banded langur social groups usually consist of one adult male with several adult females and their offspring (Ang et al., 2021a), and research within the colobine family is not indicative of long-term male tenure of breeding partners (Lees et al., 2014).
Age of first offspring for males and females	6 years	In Raffles' banded langur although the age of sexual maturity is unknown, individuals are classified as juveniles until at least age five (Ang, 2010). Six years is a best estimate based on studies of Thomas' langurs *P. thomasi* (Van Hooff et al., 2005; Wich et al., 2007).
Maximum lifespan	20	For *P. thomasi*, the maximum age in a long-term study on wild populations was estimated to be a female aged 20 (Wich et al., 2007).
Mortality rate (SD in % mortality due to EV)	7% for juvenile males aged 1–2, 10% for sub adult males aged 4–5, 0% for all other age sex classes. SD in mortality due to EV was set to 0 for all age-sex classes.	There was tracking of 11 Raffles' banded langurs groups ranging from sizes 1 to 13 from 2017 to 2021 (Ang & Jabbar, unpublished) with two mortalities observed in the five years tracking period: one in a subadult male aged 4–5, and one in a juvenile male aged 0–1 (Ang & Jabbar, 2022). Without an age sex breakdown for the population, stable age distributions assigned in VORTEX were used as a best estimate of the number of juveniles (3) and sub-adult males (2) in the population of 68. One juvenile mortality was therefore a third of the juvenile population, and one sub-adult male 50%. These were divided by the five-year tracking period to give yearly averages of 7% for juvenile males, and 10% for sub-adults. With no incidences of morality observed in other age-sex classes during the five-year tracking period, rates were set to zero. This approach is similar to that used to estimate mortality rates in a PVA on cao vit gibbons (Fan et al., 2013).
Maximum age of reproduction	20	Research in *P. thomasi* suggests that although fertility may decline with age, there is not a clear post-reproductive period (Wich et al., 2007).
Maximum number of broods per year	1	The typical interbirth interval is 1.5–2 years in *P. thomasi* (Wich et al., 2007) and was estimated to be two years in the previous Raffles' banded langur PVA (Pitra et al., 1995).
Maximum number of progeny per brood	1	The typical maximum birth rate is one infant per female in *P. thomasi* (Wich et al., 2007) with twins also stated to be extremely rare in Raffles' banded langur (Pitra et al., 1995).
% of females breeding (SD in % breeding due to EV)	25% (15%)	The only reproductive data for Raffles' banded langur is from a study between 2008–2010, in which at least six infants were observed in an estimated population of 40 (Ang, 2010), equating to an annual mean birth rate of 10% (range 5–20%). For *P. thomasi,* mean birth rate was 0.44 in a long-term study of a wild population (Wich et al., 2007). 25% ± 15% gives the most adequate range to take into account mean lower and upper estimates.
Carrying capacity (K)	247	Current habitat is 8.6 km^2. Mean group home range size estimates in *Presbytis* species is 0.43 km^2 (range 0.21–1.1 km^2) (Yeager & Kirkpatrick, 1998; Ehlers Smith et al., 2013; Hanya & Bernard, 2016). Vocalisation research from Ang (2010) is suggestive of smaller home ranges in this species so 0.21 km^2 is used as a best estimate.

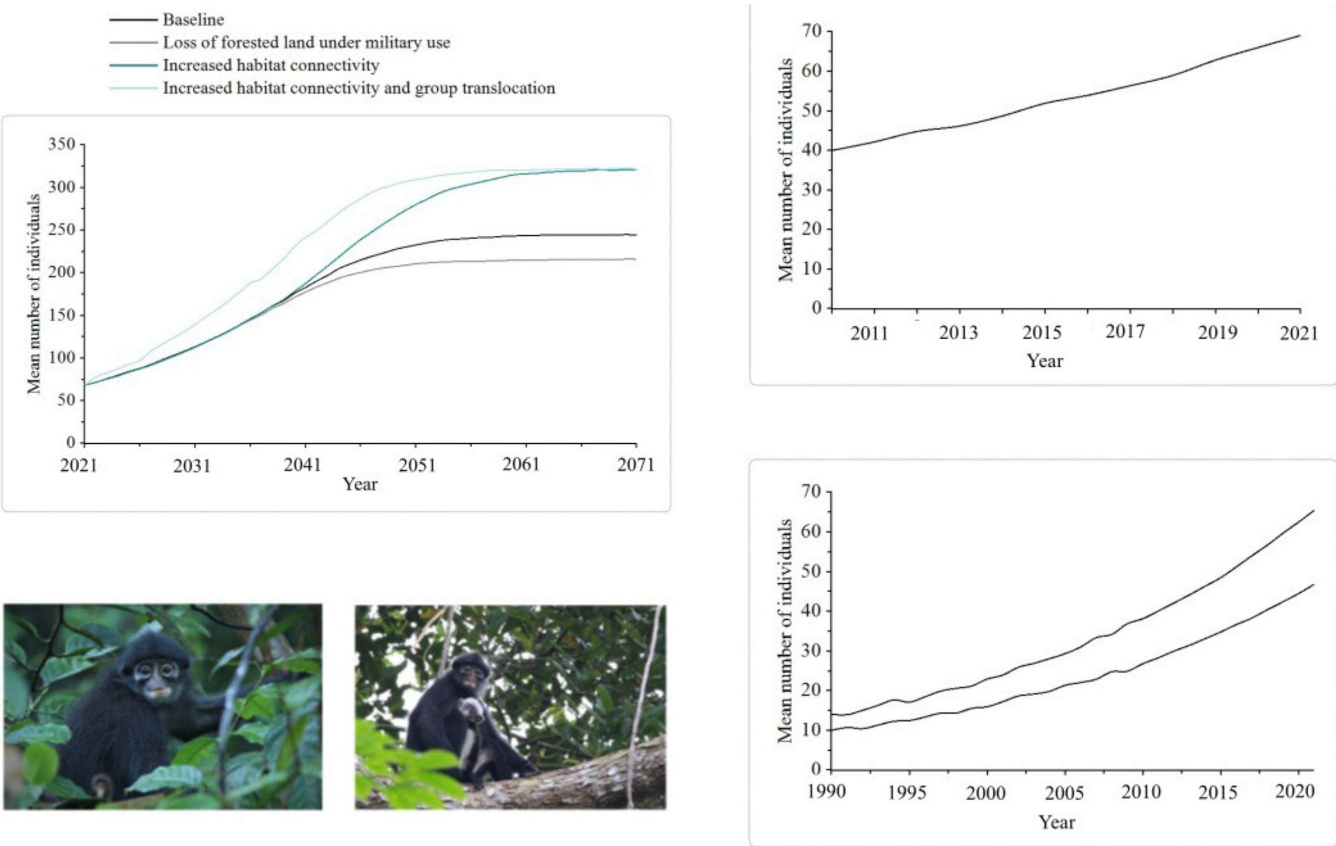

Fig. 1. Top left: baseline scenario shown with threat and management scenarios found to markedly impact upon population growth, run for 500 iterations over a 50-year period and showing the mean number of extant individuals for each. Top right: a retrospective analysis using parameters from the baseline scenario with estimates of 40 individuals in 2010 to predict the current population in 2021. Bottom right: a retrospective analysis using parameters from the baseline scenario with estimates of 10–14 individuals in 1990 to predict the current population in 2021. Bottom left: The Raffles' banded langur. Photos: Sabrina Jabbar.

under military use had the largest impact on the Raffles' banded langur population out of any threat, with the mean number of extant individuals reduced by 11% from 244 to 216 (Table 3; Fig. 1).

Management scenarios. Increased habitat connectivity resulted in a 32% increase in the mean number of extant individuals in comparison to the baseline model, from 244 to 321 individuals (Table 3; Fig. 1).

Supplementation with a single adult male had a negligible impact on the model (Table 3). Supplementation with a group increased the stochastic growth rate by 10% (change in r = 0.005) (Table 3). When group supplementation was combined with increased habitat connectivity, there was a 32% increase in the mean number of extant individuals in comparison to group supplementation as a stand-alone intervention, from 244 to 322 individuals (Table 3; Fig. 1).

The population had a 0% probability of extinction in every scenario and retention of genetic diversity did not vary markedly between the baseline model and threat and management scenarios (Table 3). The model showed that the population may reach its carrying capacity within the next 50 years for all threat and management scenarios. The minimum estimated time taken for the population to reach carrying capacity was lowest for the management scenario of a group translocation (35 years). Increasing habitat connectivity did not markedly reduce the time taken to reach carrying capacity in comparison to the baseline model, with the population still estimated to reach carrying capacity within 47 years (Table 3).

DISCUSSION

Appropriateness of the PVA model. The two key goals of this PVA were to assess the relative impact of threats and the effectiveness of management scenarios on population growth in the Raffles' banded langur population in Singapore. A lack of life history information can limit the reliability of a PVA (Frankham et al., 2010) and although specific knowledge of maximum lifespan, reproductive ecology, and home range was missing for the Raffles' banded langurs, data from closely related species were available. There were detailed species-specific records for factors including population estimates, and groupings by sex. Home range estimates chosen were within the smaller known range for the genus *Presbytis* with subsequent carrying capacity predictions likely to be optimistic.

In our retrospective analyses from previous population estimates in 1990 and 2010, the baseline model was able to accurately predict growth trajectories towards population

Table 3. Results from baseline, management and threat scenarios for the Raffles' banded langur population in Singapore (500 iterations over 50 years) N-extant, mean number of individuals alive after 50 years; GD, genetic diversity (mean heterozygosity) remaining as a proportion of the initial population; PE, probability of extinction; stoch-r, mean stochastic growth rate; SD, standard deviation; K, carrying capacity. Det-r (deterministic growth rate) for all scenarios was 0.050. The minimum number of years to reach K was the years taken for the mean number extant (inclusive of the upper SD estimate) to reach K for the scenario being modelled.

	Scenario	Baseline parameter changed (value)	N-extant ± SD	GD ±SD, %	PE, %	Stoch-r ± SD	Minimum mean number of years to reach K
	Baseline	As in table 2	244 ± 7	98.0 ± 0.3	0	0.049 ± 0.057	42
Threats	Loss of forested land under military use	K (reduced to 218)	216 ± 6	98.0 ± 0.3	0	0.048 ± 0.058	42
	Inbreeding low	Inbreeding depression (6.29; 50% lethal alleles)	243 ± 8	98.0 ± 0.3	0	0.046 ± 0.057	43
	Inbreeding high	Inbreeding depression (12; 50% lethal alleles)	244 ± 9	98.0 ± 0.3	0	0.045 ± 0.056	49
Management scenarios	Increased habitat connectivity	K (increased to 325)	321 ± 12	98.0 ± 0.3		0.049 ± 0.057	47
	Translocation of an individual	Supplementation (1 male aged 6 every 5 years in a 10-year period)	245 ± 6	98.0 ± 0.3	0	0.048 ± 0.057	47
	Translocation of a group	Supplementation (1 male and 4 females aged 6, 1 female aged 2–3 every 5 years in a 10-year period)	244 ± 7	98.0 ± 0.2	0	0.054 ± 0.059	35
	Translocation of a group and increased habitat connectivity	Combination of parameters for each above	322 ± 8	98.3 ± 0.2	0	0.054 ± 0.059	41

sizes that encompassed the current population estimate of 68 individuals. The accuracy of our model in predicting population growth in the retrospective analyses from previous population estimates indicates that the parameters used in our model are likely to produce reliable estimates of population growth in the threat and management scenarios modelled in this study.

The first PVA of this population (Pitra et al., 1995) predicted a 61–95% probability of extinction within 100 years. Parameters used in the first PVA were similar to ours for most aspects of the model but differed greatly for mortality rates. The 1990 PVA estimated mortality rates of 26–39% for infants and 3–10% for adults, retrieved from longitudinal studies of a Hanuman langur *Semnopithecus entellus* population in Jodhpur, India (Pitra et al., 1995). In our PVA we assigned lower mortality rates of 7% for male juveniles aged 1–2, and 10% for subadult males aged 4–5 with these figures estimated from the only incidences of mortality observed during long term tracking of the Raffles' banded langur population in Singapore between 2017 and 2021.

The main observed cause of mortality in this population in the tracking period between 2017–2021 is roadkill. Since this study was conducted, tracking of the population has continued and a further two instances of roadkill, one in a juvenile and one in a subadult male, were documented in 2022 (Ang & Jabbar, unpublished, Kow, 2022). Although these cases are relatively infrequent, they constitute 4–5% of the current population. Urban development is likely to continue to remove and fragment habitats, and will lead to increased incidences of road crossings in the future. A collaboration between the members of the Raffles' Banded Langur Working Group, which includes the National Parks Board (NParks), has enabled two rope bridges to be built (one in August 2019 and another in March 2020) across roads connecting forest in the current habitat to help reduce roadkill on a road regularly crossed by the Raffles' banded langurs with successful use observed after construction (Ang et al., 2021b; Ow et al., 2022).

Whilst every scenario resulted in a population that was viable in terms of a 0% estimated probability of extinction (Lacy, 2019) and retention of more than 90% of current genetic diversity (Frankham et al., 2010), the exact use of the term viable should relate to goals for populations being studied (Lacy, 2019). A growing population is a clear action listed within the goal of ensuring demographic and genetic viability within the species action plan for Raffles' banded langurs (Ang et al., 2016) and the PVA indicated that certain threats and management scenarios would have a marked impact on population growth and the mean number of extant individuals within a 50-year period. It should also be noted that whilst the model currently estimates a 0% probability of extinction, this does not account for the potential for events such as extreme weather and deforestation. One severe windstorm in 2011 destroyed part of the habitat of the langurs (Yee et al., 2019) and parks and reserves in Singapore are potentially subject to removal for plans such as new housing developments.

Identification of key threats. The most serious threat to the Raffles' banded langur population was the loss of unprotected habitat, with mean numbers of extant individuals reduced by over a tenth, and the population potentially reaching carrying capacity within the next 42 years.

Inbreeding depression with six and 12 lethal equivalents reduced stochastic growth rates but still resulted in mean numbers of extant individuals almost identical to the baseline model. The impact of inbreeding may be more noticeable if the carrying capacity were to be increased, with a PVA on western lowland gorillas finding inbreeding depression to have a marked impact upon extinction probabilities when carrying capacity was not a limiting factor in the model (King et al., 2014). Time frames can also have an impact (Nilsson, 2004) with it often taking several generations for the effects of low genetic diversity on populations to become apparent (Lacy, 2019).

Although 98% of initial genetic diversity was retained in all models, this is likely to already be extremely low due to the previous population bottlenecks (Ang et al., 2012; Srivathsan et al., 2016). With calculations of the actual number of lethal equivalents in a population complex rarely done (Frankham et al., 2010; Lacy et al., 2021), it should be noted that the values utilised in this model are default values recommended from studies on a wide range of captive and wild species (O'Grady et al., 2006; Lacy et al., 2021) and may not be reflective of the Raffles' banded langur population. Whilst inbreeding is not the most current threat to the population, future research could help to more accurately quantify the number of lethal alleles in this population to increase the reliability of this aspect of the model.

It is likely that mortality rates for this population are lower than those for similar species given the lack of threats from factors such as predation, hunting, and poaching for this population. Despite this, longer-term tracking of the population is likely to show higher mortality rates arising from natural causes such as injury and pathogens across other age-sex classes than the zero assigned in our current model Higher mortality rates could have a marked impact on the model; for example, adding a 5% mortality rate to all other age-sex classes in VORTEX would slow population growth, resulting in a mean number of extant individuals of 65 and reduced retention of genetic diversity from a mean of 98% to 93%. Continued and long-term tracking of this population would allow the model to be run again in the future with updated mortality rates as instances of morality arising from natural causes are documented.

Prioritisation of management scenarios. Out of the four management scenarios evaluated, only translocation of one adult male twice within a 10-year period had no marked impact on the population. A previous study investigating translocation scenarios in Cat Ba langurs found similar outcomes for single male translocations (Lees et al., 2014). Two group translocations in the same time frame had a positive effect on increasing the mean stochastic growth rate and may have benefits for increasing genetic diversity that this model is not able to demonstrate. Combining this with improved habitat connectivity led to an increase in the mean extant population by almost a third in comparison to group supplementation as a stand-alone scenario. The model shows that improved connectivity between current and potential habitats without group supplementation would also lead to an increase in the mean number of extant individuals by close to a third. Even with increased habitat connectivity, the population had the potential to reach its carrying capacity within the next 50 years.

Conservation measures arising. Whilst recent research has presented evidence conflicting with ideas that small founding populations increase the likelihood of extinction (Kyriazis et al., 2021), small populations are certainly more sensitive to extinction resulting from stochastic events and processes (Frankham et al., 2010; Ang et al., 2016; Lacy, 2019). Models of the impact of population size on long-term viability suggest that populations of at least 100 are needed to cope with demographic stochastic factors and populations of 1,000 or more individuals to cope with stochastic environmental factors (Frankham et al., 2010). Even in a best-case scenario of improved habitat connectivity, the small carrying capacity of the population is less than a third of the estimated size required to cope with stochastic environmental factors.

Similar to a PVA on cao vit gibbons (Fan et al., 2013) this study has found that habitat availability is the major factor limiting Raffles' banded langur population expansion, with the population potentially reaching its carrying capacity within the next 40–50 years. Fan et al. (2013) prioritised management solutions targeting habitat protection and expansion, with suggestions for prohibition of agricultural activities within current habitats and protection of forest corridors connecting fragments. Similar recommendations arising from our PVA within the context of Singapore are:

Prioritise establishing and enhancing connectivity between current and adjacent potential habitats to increase available habitat and reinforce efforts to ensure the adjacent state land forest (under military use) achieves protected status.

Identify potential new suitable habitat areas for the Raffles' banded langur within Singapore, with the population likely to reach close to carrying capacity within the next 50 years even with improved habitat connectivity enabling access to adjacent potential habitats.

Where possible, collect further population data to improve the reliability of future PVAs to include a) Quantifying inbreeding depression within the Singapore population to enable better modelling of low genetic diversity b) Continuation of long-term monitoring of the population to document further cases of mortality from both roadkill and natural causes, with mortality rates updated accordingly in future models c) Quantify the home range sizes of the Raffles' banded langur groups in Singapore to enable more accurate calculations of the carrying capacity of the current habitat.

Continue discussions on cross-border translocations of individuals from Malaysia, with consideration given to the potential impacts on genetic diversity.

The findings from this PVA complement the key priorities identified in the species action plan, demonstrating that protection of current habitats and reconnecting forest fragments will have the greatest impact on the future growth and viability of the Raffles' banded langur population in Singapore. Our model has also demonstrated the urgency with which this is required if current rates of population growth are to continue, in addition to an emerging need to find new habitats to allow continued population expansion.

CONCLUSION

This study demonstrates the applicability of PVAs within populations not necessarily threatened with imminent extinction. Despite a current growth trajectory in the Raffles' banded langur population in the absence of common threats such as hunting, the model presented here has shown that future growth will become limited by access to suitable available habitat in Singapore. Our findings have provided further support for actions already identified as top priorities for the Raffles' banded langur population in Singapore and highlighted the minimal impact of inbreeding on population growth over a 50-year period.

The key short-term goal for the population is protection and connectivity of current forest fragments and identification of suitable habitats for further expansion within Singapore. It is also important that current research on evaluation of home range sizes and suitable habitat availability within current habitats outlined in the species action plan (Ang et al., 2016) continues, to clarify the exact carrying capacity of each habitat and verify estimated time frames indicated in the current model.

Our PVA has analysed and identified the best management scenarios for the current population, but any actions taken must be monitored and evaluated over time and adapted if evidence changes (Lacy, 2019). If carrying capacity is successfully increased, further research could focus on identifying proportions of lethal alleles within the Raffles' banded langur population in Singapore, with recent evidence suggesting that deleterious alleles are of greater significance than low genetic diversity in predicting extinction risk in small populations (Kyriazis et al., 2021). This would allow future PVAs to model the potential benefits of group translocations more effectively in counteracting the impact of low genetic diversity, with implications for the longer-term adaptability and viability of the species (Lacy et al., 2021).

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