A Population Viability Analysis (P.V.A.) approach to the conservation of the Long-tailed Macaque (*Macaca fascicularis*)

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In consultation with:
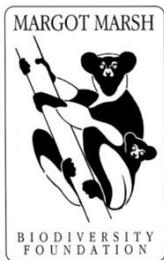The Long-tailed Macaque Project

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Executive Summary

The Long-tailed Macaque (*Macaca fascicularis*; LTM) is facing significant threats across its range in South and Southeast Asia, leading to its recent uplisting from Vulnerable to Endangered. Habitat destruction and fragmentation, coupled with population control measures such as culling and sterilisation, pose severe risks to its survival. Moreover, the species' extensive trade and use in biomedical research, is likely to exacerbate its decline. Despite being perceived as overabundant in some areas, data on local populations are often anecdotal and inconsistent, hindering effective conservation efforts.

The Long-tailed Macaque Project (LTMP), comprising around 150 researchers and conservation practitioners, initiated a Population Viability Analysis (PVA) process lead by the IUCN SSC Conservation Planning Specialist Group (CPSG) to address knowledge gaps and aid conservation efforts. The PVA process involves four key objectives: collating demographic information, analyzing threats, understanding life history stages' importance, and conducting population viability analysis.

A Threat Analysis Working Group conducted a comprehensive assessment of threats across the species' range. Participants prioritised threats based on their research experience and identified harvest for biological use, human intrusions and disturbance, residential and commercial development, and agriculture and aquaculture as the primary causes of population decline or extirpation. These threats were deemed to have a significant impact across various regions, with differing intensities and distribution.

In mainland regions, biological resource use was high in Cambodia and Vietnam, driven by harvesting for the biomedical industry and meat consumption. Human intrusions and disturbances were prevalent in Thailand and Bangladesh (where the species is presumed extinct). Agriculture and aquaculture posed a high threat in Thailand but varied across other regions.

In island regions, the severity of threats varied by location. In the Philippines, biological resource use was high in some areas due to hunting and conflict with agricultural practices. In Indonesia, Sumatra faced threats from human intrusions and disturbance, while Bali experienced medium threats from agriculture and aquaculture. Malaysian Borneo had low threat levels overall, while Peninsular Malaysia faced high threats from various sources due to frequent human-macaque interactions.

The four main threats (biological resource use, human intrusions and disturbance, and residential/commercial development) were then discussed in terms of their effects on population dynamics.

The information gathered by the Threat Analysis Working Group was then used to build a PVA model which was then used to investigate the impact of some of these threats. A baseline model of an LTM population was built in *VORTEX*. *VORTEX* is a simulation tool that factors deterministic forces, demographic events, and environmental influences affecting wild populations. It employs discrete sequential events with defined probabilities to model population dynamics. Despite its utility, PVAs like *VORTEX* offer probabilistic, not definitive, outcomes due to inherent uncertainties in wildlife population data. Consequently, caution is advised when utilizing PVA results for management decisions, emphasizing sensitivity analysis and interpretation with uncertainty in mind.

The baseline model input parameters, such as population size, breeding systems, reproductive characteristics and average mortality rates, were sourced from the most updated published and unpublished information on the species. The resulting model was discussed with the species' experts and amended based on their feedback. A demographic sensitivity analysis was run to test how different population sizes and growth rates affect viability. This highlighted the weight of the initial population size on the short and long-term extinction risk. These analyses underscored the need for accurate population estimates and comprehensive, long-term population monitoring.

The model was then used to investigate the impacts of different threats across the species' range. Given the scarcity of demographic data, the report employs case study scenarios, modelling the effects of threats under realistic conditions. These scenarios aim to provide insight into conservation management plans at national or regional levels.

Six case scenarios were defined, each representing different population sizes and threats. These scenarios served as diagnostic tools to highlight the potential impacts of threats like harvest (using a range of methods and 'quotas'), extreme weather events (with different impact and frequency), and disease outbreaks (with varying levels of lethality). Results from the simulations reveal varying degrees of vulnerability to different threats and capture methods. Harvesting adult females or entire groups can have significant long-term impacts on population viability. Extreme weather events and disease outbreaks also pose threats, with mortality rates affecting population trajectories differently across age and sex classes.

Overall, the results underscored a) the importance of females for population viability, with interventions targeting females having greater impacts.; and b) the cruciality of the initial population size in long-term viability, highlighting the need for systematic population monitoring.

Finally, the importance of interpreting results with biological knowledge and caution is emphasized. While the models provide valuable insights, they should not be the sole basis for management decisions. Instead, managers should prioritize precautionary measures, especially considering the fine line between safe and ruinous management decisions revealed by the simulations. Overall, the report underscores the need for comprehensive conservation strategies informed by robust data and stakeholder engagement.

Introduction

The Long-tailed Macaque (*Macaca fascicularis*; hereafter LTM) is widely but unevenly distributed across South and Southeast Asia (Hansen et al., 2022). In South Asia, the species is now missing from Bangladesh and is only found in the Nicobar Islands. In Southeast Asia, it occurs in the northern Rakhine region and the southern coastal lowlands of Myanmar, and east through Thailand, Cambodia, the southeastern tip of Lao, and southern Vietnam. LTM can be also found in the Malaysian peninsula and the islands of Indonesia and the Philippines.

The most recent IUCN assessment in 2022 uplisted LTM from Vulnerable to Endangered (criterion A3cd) as the global population has declined by at least 40% over the last three generations (approximately 40 years) and it is predicted to face a further 50% decline over the next three generations (Hansen et al., 2022). The species is threatened by the increasing destruction and fragmentation of its habitat (Gumert et al., 2011). Moreover, because it utilises human resources in human communities, LTM is heavily targeted by official and 'unofficial' population control measures e.g. culling and sterilization (Hansen et al., 2022). The species is also the most traded non-human primate species and the most widely used in biomedical research (Nijman et al., 2017; Shepherd, 2010).

Across its range, LTM is widely regarded as overabundant and often considered a pest, although the abundance of local populations is often overestimated and data on local population size is typically anecdotal and inconsistent (Hansen et al., 2022). As a result, populations are subjected to widespread regulated and unregulated persecution, but there is little or no evaluation of the potential effects that such measures may have at a population level (Gamalo et al., 2023). Such practices are known to have caused localised declines and extinctions, but the evidence for this is scant, although local extirpations have been documented e.g. in Bangladesh (*pers. obs.* Tanvir Ahmed, 2022) and Vietnam (Hoàng et al., 2019). The misguided perceptions and attitudes are also responsible for generally low legal protection of the species across its range (Gamalo et al., 2023). To date, no systematic or comprehensive efforts have been made to investigate the demographic dynamics of this species, particularly in response to increasing threats.

The Long-tailed Macaque Project is a Danish non-profit organisation and an international consortium of around 150 researchers and conservation practitioners working on the species across its range. In line with their statutory mission, the LTMP initiated a PVA process lead by the IUCN SSC Conservation Planning Specialist Group (CPSG), in order to address the current knowledge gap for the benefit of the species' conservation:

1. Identify and collate available demographic information on LTM
2. Undertake a structured analysis of the threats to LTM populations.
3. Understand which life history stages or age classes are more important determinants of the stability of LTM populations.
4. Use population viability analysis (PVA) to identify threats to LTM populations both in the medium and long term and their impacts on population stability.

Threat Analysis Working Group Report

Working group participants (*in alphabetical order by surname*): Tanvir Ahmed, Brooke Aldrich, Fany Brotcorne, Lief Erikson Gamalo, Gwennan Giraud, Malene Friis Hansen, Sabit Hasan, Seiha Hun, Kurnia Ilham, Lisa Jones-Engel, Nadja Ramseyer Krog, Karthi Martelli, Phaivanh Phiapalath, Brian Sabanal, Partha Sarathi Mishra, Rebecca Sweet, Bang van Tran.

Date & location: 20th August 2023 at the 29th International Primatological Congress in Kuching, Malaysia

Introduction

The initial step of the PVA process is understanding the threats to the focal species in the habitat of interest, and identifying those that are considered to have the greatest impact on the population's long-term viability. Workshop participants carried out a comprehensive semi-quantitative analysis of the types of threats acting in different regions and of the aspects of LTM's life history – reproduction, survival, dispersal, etc. – which would be most affected by these threats. The process was carried out in three distinct and consecutive phases: 1) prioritization of the known threat species (as per the latest IUCN assessment); 2) understanding of the geographical distribution and intensity of the most important threats; and 3) examining the mechanisms by which each of those threats may affect the species at a population level.

The LTM is currently listed as Endangered under criterion A3cd – (A3) Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) – I a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality (d) actual or potential levels of exploitation.

There are nine formally accepted subspecies (six of which are island endemics, Table 1) assigned to different threat categories (Hansen et al., 2022)

Table 1. *Subspecific taxonomy of the Long-tailed Macaque (Macaca fascicularis) with respective geographic ranges and IUCN Red List threat category*

Subspecies	Vernacular name	Geographical range	Threat category
M. f. ssp. atriceps	Dark-crowned Long-tailed Macaque	Khram Yai Island, Chon Buri Province, Thailand	VU
M. f. ssp. aurea	Burmese Long-tailed Macaque	Myanmar (& Bangladesh?)	VU
M. f. ssp. condorensis	Con Song Long-tailed Macaque	Con Dao National Park on Con Son Island, Hon Ba Island, Bay Canh Island and Hon Troc Island in the Con Dao Archipelago, off the coast of southern Viet Nam	EN
M. f. ssp. fascicularis	Common Long-tailed Macaque	Brunei, Cambodia, Indonesia (Kalimantan, Sumatra, Java, Bali, and most but not all offshore islands), southern Lao PDR, Malaysia (Peninsular Malaysia, Sabah and Sarawak), Philippines, Singapore, eastern and southern Thailand (and offshore islands), and southern Viet Nam	EN
M. f. ssp. fusca	Simeulue Long-tailed Macaque	Simeulue Island, off the northwestern coast of Sumatra, Indonesia	CR
M. f. ssp. karimondjawae	Karimunjawa Long-tailed Macaque	two largest islands in the Karimunjawa Archipelago, Karimunjawa Island and Kemujan Island, about 80km north of the coast of Java, Indonesia .	CR
M. f. ssp. lasiae	Lasia Long-tailed Macaque	Lasia Island, off the northwestern coast of Sumatra, Indonesia	CR
M. f. ssp. tua	Maratua Long-tailed Macaque	Maratua Island, one of the largest islands in the Derawan Islands that lie off the coast of East Kalimantan, Indonesia	CR
M. f.ssp. umbrosa	NicobarLong-tailed Macaque	Nicobar Islands, India	VU

Threat ranking

The first objective was to identify the leading causes of LTM population decline or extirpation across the range. Attendees were presented with the list of threats to the species which were identified by the most recent IUCN red list assessment (Hansen et al. 2022; Table 2). These were ordered as per the IUCN threat categorization scheme (IUCN, 2022).

Table 2. *List of threats identified by the latest Red-List assessment of the Long-tailed Macaque (Hansen et al. 2022), ordered according to the IUCN standard threat categorization scheme (IUCN 2022)*

Threat category – 1st order	Threat category – 2nd order
1. Residential & commercial development	1.1. Housing & urban areas
	1.2. Commercial & industrial areas
	1.3. Tourism & recreation areas
2. Agriculture & aquaculture	2.1. Annual & perennial non-timber crops
	2.2. Wood & pulp plantations
	2.3. Livestock farming & ranching
	2.4. Marine & freshwater aquaculture
3. Energy production & mining	3.3. Renewable energy
4. Transportation & service corridors	4.1. Roads & railroads
5. Biological resource use	5.1. Hunting & trapping terrestrial animals
6. Human intrusions & disturbance	6.1. Recreational activities
10. Geological events	10.2. Earthquakes/tsunamis
11. Climate change & severe weather	11.1. Habitat shifting & alteration
	11.5. Other impacts

Each participant was then provided with five "votes" (sticky dots) and asked to place those votes on each of the threats (1st order only) proportionally based on the following question:

"Which threats are (or have been) most directly responsible for a decline in abundance of the population in your study area/region of interest"

It was stressed to participants that they should cast their votes based on *their own* research experience in *their* area of interest. This was to *a*) avoid the temptation to vote what others have voted (i.e. informational social influence), and *b*) capture information about threats even when they were relevant to one region. For example, the threat posed by 'Geological events' received one vote from one participant who has worked in the Nicobar Islands. Although the threat is limited to a small proportion of the range, it is likely to have a large effect on the local population which is also an endemic subspecies i.e. *M. f.ssp. umbrosa* (Table 1).

This exercise allowed participants to identify four leading causes of population declines or, in some cases, possible extirpation (e.g. Bangladesh), namely harvest for *biological use*, *human intrusions & disturbance*, *residential and commercial development* and *agriculture and aquaculture* (Table 3). These results were discussed and agreed upon by all after the voting exercise. Given there was a considerable gap between the first (highest ranking) four threats and the others, participants agreed it was justified and reasonable to focus on these for subsequent phases of the threat analysis.

Table 3. *List of the threats to the Long-tailed Macaque populations in order of importance as per the voting by workshop attendants*

Threat category	Number of votes*
5. Biological resource use	24
6. Human intrusions & disturbance	16
1. Residential & commercial development	15
2. Agriculture & aquaculture	15
4. Transportation & service corridors	6
11. Climate change & severe weather	3
3. Energy production & mining	1
10. Geological events	1

* NB. As participants were free to use liberally their votes, the total number of votes and participants may not add up

Threat distribution and intensity

Participants were divided into two groups according to their geographical area of expertise: (a) those who work (or have worked) on the mainland (Bangladesh, Cambodia, Myanmar, Lao PDR, Singapore, Thailand, Viet Nam) and (b) those who have worked on islands (Brunei Darussalam, Nicobar Islands, Indonesia, Malaysia, Philippines and Timor-Leste). Not all range countries were represented. Each group was provided with an enlarged updated map of the species' habitat preference across the known range. Participants were asked to discuss and outline both the distribution and severity (Low/Medium/High) of the four key threats in their region of expertise. Participants were encouraged to consider and discuss potential differences in the protection status of the species and their habitat at a national and local scale. Finally, there was a plea to avoid discussing or exposing the identity of individuals or agencies behind some of the threats and to focus on the threats themselves. Each group appointed a facilitator, a note-taker and a spokesperson who would report to the plenary at the end of the exercise.

Mainland range

Working group participants (*in alphabetical order*):
Tanvir Ahmed, Sabit Hasan, Seiha Hun, Lisa Jones-Engel, Nadja Ramseyer Krog, Phaivanh Phiapalath, Bang van Tran.

Participants explored and discussed each threat in turn assigning it a severity score i.e. Low/Medium/High (Table 4). In the case of Bangladesh, where the species has not been seen for six years (i.e. 'missing' *sensu* Long and Rodríguez 2022), the severity of the threats was examined in relation to what it may have been in the past and likely have led to its eradication.

Table 4. *Severity (Low/green, Medium/orange, High/red) of the key threats to Long-tailed Macaques in the mainland portion of their range (NB. Bangladesh – in grey – the species is currently considered 'missing')*

Country	Biological resource use	Human intrusions & disturbance	Residential & commercial development	Agriculture & aquaculture
Bangladesh	n.a.	High	High	High
Cambodia	High	Medium	Low	Medium
Lao PDR	Low	Low	Low	Medium
Myanmar	n.a.	Low	n.a.	n.a.
Vietnam	High	Medium	Low	Low
Thailand	Medium	High	n.a.	High

The threat from harvest for biomedical use or meat consumption (**biological resource use**) was deemed to be *high* in Cambodia and Vietnam, although part of the pressure in the former is thought to be from individuals originating from the latter. In Thailand, the severity of this threat was considered *medium* although, again, activities seem to be more intense close to the Cambodian border. In Thailand, there is also the case of trapping carried out at temples where the species tends to concentrate. In Lao PDR, the current threat was regarded as *low* with only one recent documented case of capture for the biomedical industry and low levels of hunting. Nonetheless, the species population is declining in Lao PDR (Gamalo et al., 2023; Hamada et al., 2011). There was no

information on Myanmar, whereas the discussion was not relevant to Bangladesh since the population is currently considered 'missing' (see Long and Rodríguez 2022) from the country.

Human intrusions and disturbance were mainly discussed considering three different aspects: recreational, feeding from humans and pressure from tourism. These types of pressure were considered *high* in Thailand and Bangladesh (vehicle movement for tourism) before the species went missing. The severity of the threat was deemed to be *medium* in Cambodia and Vietnam, where LTMs are often seen to crowd along roads and tourism sites. Conversely, these pressures are thought to be *low* in Lao PDR due to a lack of tourism activity, and in Myanmar due to the current army operations (including bombing).

Land conversion for **residential and commercial development** was deemed to be *high* in Bangladesh. This may have been one of the factors driving LTM to its likely extirpation as well as preventing it from recolonizing the country from bordering Myanmar. Besides the conversion of the land for residential and commercial purposes, the southeast region of Bangladesh has seen further development (mostly removal of mangroves) for the building of a harbour and other recreational structures. In other areas, amidst the deterioration of the security status, army and refugee camps were created. In Cambodia (except for the fast-developing Preah Sihanouk Provincial Town), Lao PDR (except for Nam Kong hydropower plants; Phiapalath and Hansen 2023), and Vietnam, the threat is considered to be *low*. There was no information on Myanmar and Thailand.

Threat from **agriculture and aquaculture** was thought to be *high* only in Thailand, whereas it was deemed to be *medium* in Cambodia and Lao PDR, and *low* in Vietnam (although growing).

Participants made an effort to map the distribution of the above threats across the range to facilitate their discussion on their levels of severity at a national scale (Fig 1).
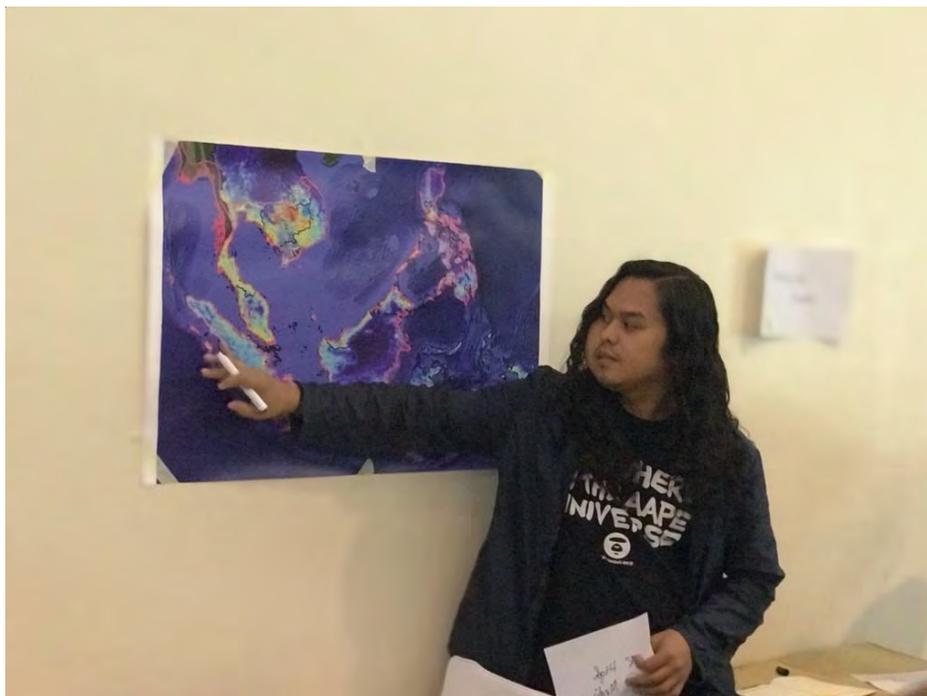
Figure 1. *Participants used updated maps of the species distribution to aid the discussion on regional severity of different threats (Photo Simon Valle/CPSG)*

Island Range

Working group participants (*in alphabetical order*): Brooke Aldrich, Fany Brotcorne, Lief Erikson Gamalo, Gwennan Giraud, Kurnia Ilham, Brian Sabanal, Partha Sarathi Mishra, Rebecca Sweet.

Date & location: 20th August 2023 at the International Primatological Congress in Kuching, Malaysia

The working group on the island portion of the range approached the problem by discussing threat distribution and severity island by island (rather than threat by threat) as they deemed that would be the smallest relevant unit (Table 5).

Philippines

Overall the threat level from **biological resource use** (including killing and hunting due to conflict with agricultural practices) was deemed *high* i.e. *low* in Puerto Princesa on Palawan Island; *medium* in Tanay, Rizal, on Luzon Island; Hindang Nature Park, Leyte Visayas Islands; and Makilala, North Cotabato, on Mindanao Island, but *high* in Zamboanga del Norte, on Mindanao Island; and Banton Island, on Romblon island. The severity of **agriculture and aquaculture** as a threat was considered to be *medium* (although specific concerns were raised for the population in Tagum City, Davao del Norte on Mindanao Island; L. Gamalo *pers. comm.*) and *low-medium* for **residential and commercial development**. The case of heavy persecution in Romblon (actively encouraged by per-tail bounties) was discussed as a case where the direct harvest (biological resource use) is caused by the widespread conversion of habitat to coconut plantations and resulting conflict due to crop raiding. The threat from **human intrusions and disturbance** was deemed *low* overall, although concerns were raised for the possible effects of the uncontrolled macaque tourism present at Hindang Nature Park, Leyte (an unprotected area) which may be compounded by the restricted movement ability due to habitat fragmentation and agricultural development.

Indonesia

Sumatra & Java:
The threat from **human intrusions and disturbance** and **agriculture and aquaculture** in Sumatra is *high* but only because they lead to retaliatory killings i.e. **biological resource use.** The severity of this threat varies across the island depending on the local cultural and religious traditions e.g. in the Sumatran states of Riau, West Sumatra, and Jambi the consumption of LTM meat is forbidden. This threat is deemed to be *high* in N Sumatra and *medium* over the rest of the island. The species is *high*ly threatened by capture for the biomedical industry in Java.

Bali

The threat from **biological resource use** is low due to the cultural background of Bali's inhabitants i.e. Balinese Hinduism. **Human intrusions and disturbance** have a low severity, mostly in the form of heightened likelihood of conflictual interactions with humans as well as increased risk of disease transmission and outbreak (voluntary or accidental food supplementation by humans is responsible for localised high population densities). The severity of the threat from **agriculture and aquaculture**

and **residential and commercial development** was deemed to be *medium*. However, due to continued conversion and loss of LTM habitat, there is an increasing number of negative interactions between humans and macaques which, in turn, have sometimes resulted in culling.

Malaysia

All threats were considered to be *low* in Malaysian Borneo.
On the other hand, in Peninsular Malaysia, threats from **biological resource use**, **human intrusions and disturbance** and **residential and commercial development** were deemed to be *high* as relocations and culls are frequent in developed areas where humans and macaques come into contact.

India (*Nicobar Islands*)

Great Nicobar Island is for the great majority (95%) forested and has a relatively small human population ~ 8,000 - 10,000 people). Thus, the current threat from direct **biological resource use** is negligible. However, the recently approved plans to build a large port are likely to increase significantly the human population (up to about a million people) and major changes are anticipated i.e. *high* threat from **agriculture and aquaculture** and **human intrusions and disturbance**. There is serious concern that the local subspecies (*Macaca fascicularis umbrosa*) may not be able to survive such sudden pressure. The islands and their ecosystems are also very vulnerable to earthquakes and tsunamis (see Table 3, **Geological events**) a threat that is not concerning for the species as a whole but could be fatal to the subspecies in Nicobar Islands.

Table 5. *Severity (Low/green, Medium/orange, High/red) of the key threats to Long-tailed Macaques in the island portion of their range*

Country	Islands	Biological resource use	Human intrusions & disturbance	Residential & commercial development	Agriculture & aquaculture
India					
	Nicobar Islands	Low	Low	Low	Medium
Indonesia					
	Sumatra & Java	High	High	n.a.	High
	Bali	Low	Low	Medium	Medium
Malaysia					
	Peninsular Malaysia	High	High	High	n.a.
	Borneo	Low	Low	Low	Low
Philippines		High	n.a.	Low	Medium

Threats' effects on population dynamics

In a plenary session, participants were encouraged to discuss and share the mechanisms by which each of those threats may affect the species at a population level across the range. Threat categories were explored and reviewed one at a time.

Biological resource use

Direct harvest of individuals, whether for food consumption, for the pet trade or for use in the biomedical industry, was deemed to be the most severe of all threat categories. However, the removal of individuals from the population is carried out in different ways depending on the area and the final use. One widespread technique is to harvest a whole troop of LTM by targeting the tree where they spend the night and clearing the surrounding trees to prevent them from escaping. This technique is used in Cambodia (Hun et al., 2003), Indonesia (mostly Java and Sumatra) and Vietnam, and it is preferred for yielding a large number of individuals to be used for biomedical experimentation. Another technique for capturing high numbers is with large traps, however, these tend to capture mostly young males (juveniles and subadults) due to them being more prone to taking risks. In Sumatra, α-males are known to be targeted for food by virtue of their larger size or to use in captive breeding. However, this is normally unlikely to be successful for more than three individuals from the same troop as the remaining individuals would quickly become wary and elusive. This doesn't stop harvesters from focusing on different troops in the same population, allowing for a sustained and consistent removal of individuals (M. Friis Hansen *pers. comm.*). Delegates from Cambodia and Vietnam report cases where LTMs are killed as accidental or opportunistic bycatch, e.g. in snares or during hunts, respectively. It is hard to quantify these incidents and they are likely to affect different sexes and age classes at random. When this involves females with infants, the infants are nearly always sold to the pet trade. Because of this, the capture of adult females is highly valued also as they are prized as breeders in captive raring facilities. In Bali, due to the religious context (82% of the population is Hindu), the killing of LTMs is taboo, so problematic individuals (those who have had negative interactions with humans) are caught and removed from the population but not killed (in some cases these are returned to the population after a being kept for some time in captivity as a 'punishment' for their misdeeds). In the Nicobar Islands, although rare, there have been reports of large males (regardless of status or group of prevenience) being caught to be sold to zoos.

Human intrusions & disturbance

One of the key causes of human intrusion and disturbance was identified in tourism which often entails the proactive or accidental provision of food. An immediate consequence of this is high exposure to human-mediated diseases and accidental poisoning. The medium- to long-term effect is the progressive habituation of the macaques to human presence. Habituation increases the chances of negative interactions between the species and humans. As encounters become more frequent monkeys are occasionally killed and injured, mostly by vehicles along the roads where food is provisioned. Finally, the concentration of any individuals within relatively restricted areas can increase the number of intra-specific hostile interactions which can result in heightened mortality rates. Given its unique cultural background, in Bali, there is additional potential disturbance due to crowded ceremonies which take place in the same outdoor temples where the LTMs concentrate.

Some human disturbance is thought to be exercised indirectly due to the introduction of escaped individuals of the same species (likely host of human-mediated diseases), hybridisation with Pig-tailed Macaque (*Macaca leonina*) or introduced Rhesus Macaques (*Macaca mulatta*) as well as the ceremonial release of other species (e.g. small mammals) in Bali i.e. Tumpek Kandang ceremony (G. Giraud *pers. comm.*).

Concern has been expressed about the fact that human encroachment and human-mediated movement of LTMs, may have increased (beyond naturally occurring rates) the instances of hybridization i.e. inter-specific hybridization with Pig-tailed Macaque in Cambodia and Lao PDR, and intra-specific cross-breeding between Burmese (*M. f. aurea*) and common LTMs (*M. f. fascicularis*) in Southern Thailand (G. Giraud *pers. comm.*).

Residential & commercial development + Agriculture & aquaculture

It was agreed by LTM experts that there is great overlap in the mechanisms by which Residential & commercial development and Agriculture & aquaculture threaten LTM populations. Thus, the two were discussed and reviewed jointly.

The pressure from these two threats is likely to lead to two seemingly opposite consequences. On one hand, the degradation and destruction of LTM's natural habitat is likely to decrease their access to the necessary resources i.e. food and space. On the other hand, the proximity to residential, commercial and agricultural development would expose LTMs to unnaturally high concentrations of resources which would boost the population. In both cases, the result is likely to be some unusually abundant populations in localised and restricted suitable areas competing for food and space. This, in turn, may increase the chances of exposure to diseases (and potential related outbreaks) and parasites (both human-mediated and non). In these conditions, LTMs are expected to be more likely to enter into conflictual interactions with humans which would result in negative public perception and direct persecution. It was discussed how, in some cases, this situation may also result in inflated estimates of abundance. As LTMs dwell in and around anthropogenic habitats they are also more likely to come in contact with dogs which are known to attack and occasionally kill macaques (the last LTM in Bangladesh is thought to have been killed by a stray dog). A peculiar case of 'development' is to be found in Bangladesh where refugee camps have rapidly proliferated within the LTM range in response to the humanitarian crisis in neighbouring Myanmar. Finally, LTMs would be exposed to the negative effects of pesticides, power lines (electrocution accidents) and roads. In many cases, conservation efforts to oppose agricultural or infrastructure developments have been hampered by a strong political will to address food security and the production of clean energy, respectively.

Population Modelling

The *VORTEX* computer model is a PVA simulation model of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild populations. *VORTEX* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modelled as constants or random variables that follow specified distributions. The package simulates a population by stepping through a series of events that describe the typical life cycles of sexually reproducing, diploid organisms.

PVA methodologies such as the *VORTEX* system are not intended to give absolute and precise 'answers', since they are projecting the interactions of many randomly fluctuating parameters used as model input and because of the considerable uncertainty we observe in typical wildlife population demography datasets. Because of these limitations, many researchers have cautioned against the sole use of PVA results to promote specific management actions for threatened populations (Beissinger & McCullough, 2002; Ellner et al., 2002; Lotts et al., 2004; Ludwig, 1999; Reed et al., 2002). Instead, the true value of an analysis of this type lies in the assembly and critical analysis of the available information on the species and its ecology, and in the ability to compare an array of possible scenarios theorised through the methodical variation of key parameters in the demographic model of a given species i.e. sensitivity analysis (Mills & Lindberg, 2002). PVAs can be extremely useful to conservation biologists as a secondary source of analysis if results are conservatively interpreted in terms of uncertainty (Reed et al., 2002).

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The *VORTEX* system for conducting population viability analysis is a flexible and accessible tool that can be adapted to a wide variety of species types and life histories as the situation warrants. The program has been used around the world for both teaching and research applications and is an accepted method for assisting in the definition of practical wildlife management methodologies. Nonetheless, the interpretation of the output should depend upon the best available knowledge of the biology of the species in its habitat, the environmental conditions affecting it, and possible future changes in these conditions. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Lacy (2000) and Lacy, Miller, and Traylor-Holzer (2021)

POPULATION

Population refers here to the total number of individuals of the same species (i.e. capable of interbreeding) within a specific geographical or ecological boundary i.e. sharing common characteristics and residing in a particular habitat with minimal or no fragmentation (Wells & Richmond, 1995). The models used do not take into account the partitioning of said population in groups which, in the case of LTMs, are variable in size, and subject to fission-fusion dynamics depending on resource availability (Gumert et al., 2011).

Baseline Input Parameters for Stochastic Population Viability Simulations

Much of the demographic data used as input to our LTM population dynamics models is derived from the published literature and some unpublished data. A first version of the baseline model was presented for feedback in a series of dedicated meetings at the International Primatological Congress in Kuching (19th - 25th August 2023) to a group of key experts on the species ― (in alphabetical order by surname): Fany Brotcorne, Lief Erikson Gamalo, Eva Gazagne, Gwennan Giraud, Michael D. Gumert, Seiha Hun, Kurnia Ilham, Lisa Jones-Engel, Laurie Patouillat, Nadja Ramseyer Krog, Partha Sarathi Mishra, Rebecca Sweet.

Baseline population model

The baseline population model was developed based on the best available (published and unpublished) knowledge of the biology and demographics of the species. The model and its parameters were subjected to the scrutiny of and agreed upon by the experts gathered in the above-mentioned workshop. The resulting model had a λ of 1.06. Although realistic, this was deemed to be representative only of particularly abundant and healthy populations, and it was agreed that a second baseline model would be useful to provide better insight into those populations which exhibit only slight population growth over time. Thus all consecutive analyses were performed using two alternative baseline models i.e. slow-growing, $\lambda = 1.02$ and, fast-growing $\lambda = 1.06$.

A word of warning about the baseline population model

The baseline population model is a representation of the biological and demographic potential of the species in ideal/theoretical conditions which is devoid of natural and anthropogenic threats. This, by no means, is a realistic depiction of any specific real-world population as the model lacks key ecological elements such as inbreeding, etc (*see below*).

Population

The target unit of PVA is a 'population', which is here defined as a group of individuals of the same species inhabiting a specific geographic area that is not fragmented. This definition includes all subpopulations which have the possibility of exchanging individuals and interbreeding. This analytical approach serves as a bridge between theoretical ecological principles and practical conservation strategies. In the case of the LTM, the population (particularly large ones) is likely to be comprised of several troops which may exchange individuals. However, the population as a unit does not experience any emigration or immigration. Thus the interpretation of the results has to take this into account e.g. matching real-world management problems with the closest simulation model in terms of size.

Breeding System

LTM display a short-term polygynandrous breeding system (in which a female pairs with several males, each of which also pairs with several different females) with a high level of male dispersal while females are typically philopatric (stay in the group they were born into) in nature (Melnick & Hoelzer, 1992; Tosi et al., 2003). The (short-term) polygynous option was selected in the model as the best representation of the species breeding system.

Age of First Reproduction

VORTEX considers the age of first reproduction as the age at which first offspring are produced, not simply the onset of sexual maturity. Published evidence shows that although females have been known to reproduce earlier, they normally start at four years of age, whereas males are not sexually active before they are six (van Noordwijk & van Schaik, 1999). This information was supported by the experts present at the workshop.

Age of Reproductive Senescence

In its simplest form, VORTEX assumes that animals can reproduce (at the normal rate) throughout their adult life until a set '*Maximum age of reproduction*'. In many primate species, senescence affects the ability of individuals to reproduce with a consequent lag between their maximum age of reproduction and their lifespan (Comizzoli & Ottinger, 2021; Milich et al., 2020).
However, the workshop participants suggested that the maximum age of reproduction and maximum lifespan are likely to coincide in the LTM as they shared and agreed upon anecdotal knowledge of 'very old' individuals breeding as well as little of no observation of non-breeding individuals. Observations from Cambodia suggest that, although individuals can breed in old age, only some will eventually bear young in the reproductive season suggesting that older individuals may not be as fertile or effective in producing viable offspring (Seihan Hun *pers. comm.*). Bearing in mind that this parameter requires the maximum age, this was kept as the maximum of the lifespan (*see below*), minus one year.

Maximum lifespan

The only study which quantifies the maximum lifespan of free-ranging LTMs was conducted on a population outside of the species' native range (i.e. Florida, U.S.A) and it measured a median lifespan = <15 years showing that <5% of the individuals reach 25 years of age (Johnson & Kapsalis, 1995). Workshop participants agreed that a number between 20 and 25 would be a fair estimate of the species' maximum lifespan in the wild. Because of this, a final maximum lifespan of 23 years of age was set in the model. However, because empirical data from 'truly wild' populations is hitherto unavailable, it was hypothesised that lifespan could be significantly longer i.e. ~30 years. Thus, a number of tests were carried out to ascertain the relative (negligible) effect of this parameter on subsequent analyses and their results (see *Appendix I*).

Offspring Production

Starting at age 4 or 5 LTM females can give birth a maximum of only once a year and typically can produce one infant every 18-28 months until they reach the late teens when the interbirth interval lengthens. Twin births are extremely rare (e.g. long-term work in Bali anecdotally recorded 2-3 cases in 5 years; G. Giraud *pers. comm.*, or 5-6 cases in 30 years A. Fuentes *pers. comm.*) and in most of those instances, one of the individuals dies (Michael Gumert *pers. comm.*). Thus experts agreed that setting the 'maximum number of progeny per birth' at 1 is a fair representation of the species' biology.

The available published data on the sex ratio at birth indicates a mean of 53.6% of males (Giraud et al., 2021; Pal et al., 2018; van Noordwijk & van Schaik, 1999; Vrazila et al., 2022).

Published papers provided figures on the number of young per female per year (fertility rate) i.e. mean ± SD = 53 ± 3 (Giraud et al., 2021; Pal et al., 2018; van Noordwijk & van Schaik, 1999; Vrazila et al., 2022). Given that only one individual is produced per birth (*see above*), this value was input in the model as the percentage of adult females breeding per year. Infants are dependent on the mother for the first year and a half of their life, a time in which she will not be available for reproduction. To this effect, an 'individual state variable' was integrated into the model so that females do not breed again until the offspring is two years of age (Lacy, Miller, and Traylor-Holzer 2021) i.e. 1.5 years + 5.5 months gestation.

Male Breeding Pool

In many species, some adult males may be socially restricted from breeding despite being physiologically capable. This can be modelled in *VORTEX* by specifying a portion of the total pool of adult males that may be considered available for breeding each year. Observations of LTMs suggest that all adult males are equally capable of pairing with an adult female when necessary. We therefore set the probability of an adult male entering the breeding pool as 100%.
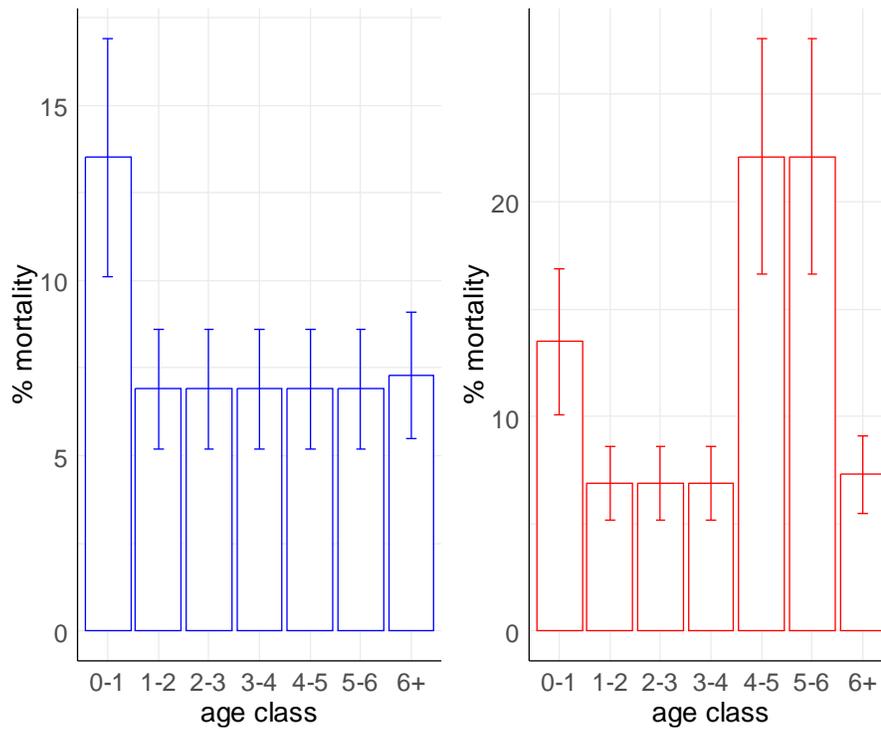
Mortality

Information on mortality rates for different age classes was sourced from available published data across a number of species and is summarised in Table 6.

Table 6. *Sex- and age-specific mortality rates and Environmental Variation for Long-tailed Macaques with respective sources. N.B. SD values refer to the average between studies.*

Age class	Sex	Mortality rate % (± SD)	EV	Source
0-1	♂/♀	13.5 ± 8.35	3.4	van Noordwijk and van Schaik 1999 Vrazila, Sumarga, and Ramdan 2022
1-4	♂/♀	6.9 ± 3.8	1.7	Vrazila, Sumarga, and Ramdan 2022 van Noordwijk and van Schaik 1999 Santosa et al. 2012
4-6	♂	22.1 ± 0.59	5.5	Vrazila, Sumarga, and Ramdan 2022
Adult	♂/♀	7.3 ± 5.7	1.8	van Noordwijk and van Schaik 1999

VORTEX requires a measure of environmental variation (EV) to model the yearly fluctuations in the probabilities of survival that arise from random changes in environmental conditions. EV impacts all individuals in the population simultaneously. However, none of the sources provided a measure of interannual variation of mortality, thus an arbitrary 25% of EV was applied for mortality across age classes.

The distribution of mortality across age classes (Figure 2) was reviewed and discussed with LTM experts who endorsed them to be the best available data as well as a fair depiction of the species demography.

Figure 2. *Distribution of mortality across age classes for females (left) and males (right). Error bars show the respective Environmental Variation (EV) used in the model i.e. 25%.*

Catastrophes

No catastrophes were included in the baseline model. The effect of catastrophes was later explored in the scenarios (see § *Phase 2: case scenarios*)

Inbreeding depression

There is currently no data on the mode of action of inbreeding depression in wild LTM populations, or even if inbreeding depression exists at all. Therefore, it is impossible to quantify the role this process may play in LTM populations. Because of this, we did not include this variable in the baseline model or any successive analyses.

Mate Monopolisation

In each reproductive season, 100% of males are known to reproduce with high levels of promiscuity exhibited by males and females alike. However, evidence shows that paternity is mostly in favour of dominant males (De Ruiter et al., 1994; Engelhardt et al., 2006).

Carrying Capacity

The carrying capacity (K) for a given habitat patch defines an upper limit for the population size, above which additional mortality is imposed randomly across all age classes in order to return the population to the value set for K. Carrying capacity is typically very difficult to estimate in the field for any species. Our baseline model is designed to allow unrestrained growth of the population beyond its initial size, thus K was set to an overgenerous purely theoretical 20,000 individuals i.e. larger than any known LTM population

Initial Population Size, Iterations and Years of Projection

All population projections (scenarios) were simulated 500 times with an arbitrary initial population size of 600 individuals. Each projection extends to 100 years, with demographic information obtained at annual intervals. 100 years was deemed a suitable timescale to evaluate the long-term viability of populations for long-lived species such as the LTM. All simulations were conducted using *VORTEX* version 10.5.6. (Lacy and Pollack 2022).

Table 7. *Demographic input parameters for the baseline VORTEX model for the Long-tailed Macaque across its native range. See the accompanying text for more information.*

Model Input Parameter	Baseline value
Breeding System	Polygynous
Age of first reproduction (♀ / ♂)	4 / 6
Maximum age of reproduction	23
Inbreeding depression?	No
Annual % adult females reproducing (SD)	53 (3)
Overall offspring sex ratio	0.53.
Adult males in breeding pool	100%
% annual mortality (EV)[‡]	
0-1 ♂/♀	13.5 (3.4)
1-4 ♂/♀	6.9 (1.7)
4-6 ♂	22.1 (5.5)
Adult ♂/♀	7.3 (1.8)
Catastrophe?	No
Initial population size	50
Carrying Capacity (K)	$+\infty$

Phase 1: Demographic sensitivity analysis

During the development of the baseline input dataset, it quickly became apparent that one key source of uncertainty is the size of the different populations. This is because (a) population estimates are few and often vary greatly in their methods and level of precision, and (b) such estimates are likely to vary of different orders of magnitude across the range with likely profound effects on their long-term viability.

Thus, a series of analyses was carried out to test the relationship between growth rate and vulnerability of different population sizes. This type of analysis tests the sensitivity of our models to the uncertainty of the population size and can be an invaluable aid in identifying priorities for detailed research and/or management projects targeting specific elements of the species' population biology and ecology. To conduct this demographic sensitivity analysis, a selected set of finite population growth rates ($\lambda = 1$, $\lambda = 1.04$, $\lambda = 1.07$, $\lambda = 1.1$) and population sizes ($N_0 = 25$, 50, 100, 250, 500, 1000) we identified. This allowed for the construction of a total of 24 alternative models whose viability (defined, for example, in terms of 'probability of survival) can be compared.

Results of Simulation Modelling

Baseline simulation

Where appropriate, the results that are reported here for each modelling scenario include:
r_s (SD) – The mean rate of *stochastic population growth* or decline (standard deviation) demonstrated by the simulated populations, averaged across years and iterations, for all simulated populations that are not extinct. This population growth rate is calculated each year of the simulation, prior to any truncation of the population size due to the population exceeding the carrying capacity.
PE – **Probability of population extinction** after the specified time interval (in years), determined by the proportion of specified iterations within that given scenario that have gone extinct within the given time frame. "Extinction" is defined in the *VORTEX* model as the absence of either sex.
N(extant) and N (SD)– These are two distinct measures of mean population size after the specified time interval (in years), averaged across all simulated populations, excluding and including those that are extinct respectively.
**T(E)** – The average time to population extinction, in years.

The set of demographic, and ecological input data that represents our best understanding of the life history of LTM populations across their range, is hereafter referred to as our *baseline model*. In this case, our baseline model simulates the predicted trajectory of an initial theoretical population of 50 individuals that is free of the impacts of catastrophe and genetic sources of mortality (i.e., inbreeding depression). The results of this analysis are presented in Table 8 and Figure 3. The finite population growth rate (λ) is 1.061, and the extinction probability over 100 years is 0.0%.

The PVA working group thought that the simulation of LTM population dynamics was acceptably accurate, both in its mean trajectory and in its manifestation of annual variability in demography and subsequent population growth. We therefore felt comfortable with proceeding into the demographic sensitivity analysis phase of our work with the baseline model after the few adjustments suggested were taken on board and integrated into the model.

Table 8. Key results of simulating the baseline models over 100 years with an initial population of 600 and a λ = 1.06 and λ = 1.02 — simulations were run 500 times. rs = stochastic growth rate, SD(rs) = standard deviation of the stochastic growth rate, PE = probability of extinction, N(extant) = mean size of population after 100 years (excluding extinction events), SD(N(extant)) = standard deviation of the mean size of population (extant) after 100

years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction

λ	N_0	r_s	SD(r_s)	PE	$N_{(extant)}$	SD($N_{(extant)}$)	N	SD	Med. TE	Mean TE
1.02	600	0.0064	0.0507	0	1194.12	436.13	1194.12	436.13	0	0
1.06	600	0.0499	0.0341	0	1996.14	17.11	1996.14	17.11	0	0
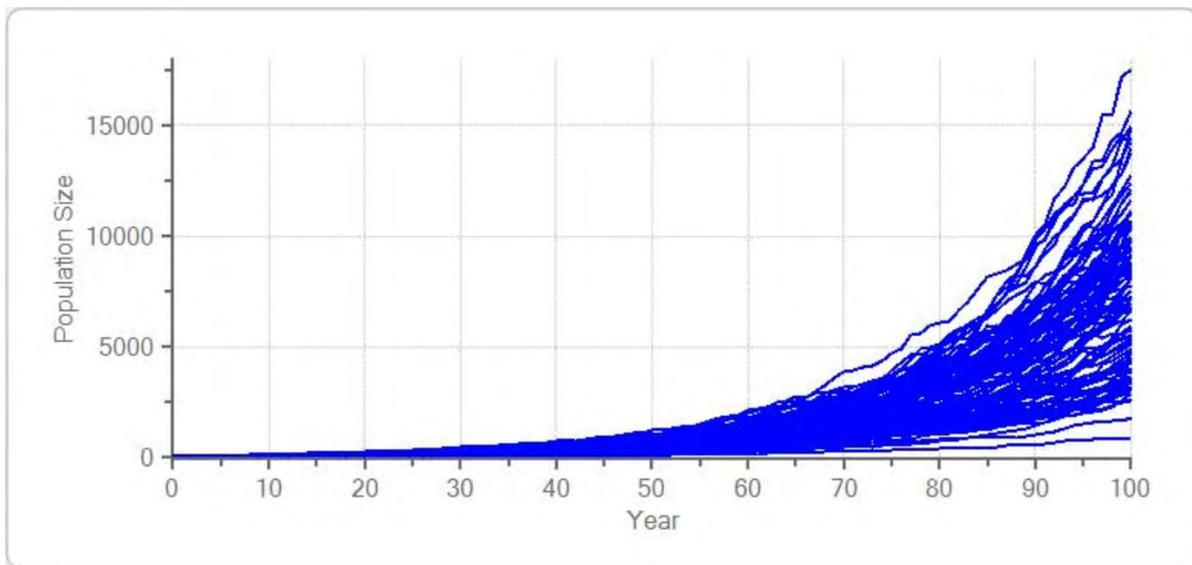
Figure 3. *Example of 100 randomly sampled iterations of the baseline VORTEX simulation model of LTM with a λ of 1.06, The average stochastic rate of population growth (±SD) is 0.05 ± 0.04*

It is important to note that, despite our sense of comfort with this model, these baseline projections are merely a starting point for a deeper analysis of LTM population viability. These models are by no means descriptive of the predicted fate of any one population or class of populations currently known to exist in Southeast Asia.

Risk analysis I: Population size, finite population growth (λ) and extinction risk

The relative extinction risk as a function of population size, and finite population growth (λ) was explored. This analysis was aimed at estimating, for each λ, a population size threshold, below which the risk of extinction was likely to be unacceptably high.

To conduct this analysis, a suite of four models was developed with a λ of 1,00, 1, 02, 1.04, 1.07 and 1.1 These were derived from the baseline model by altering mortality rates proportionately across age classes i.e. +67%, +45.6%, +23%, -11.8% and -55.6%, respectively. Each of these was then

tested with different initial population sizes i.e. increased from 5 to 1000 in defined increments (N_0 = 25, 50, 100, 250, 500, 1000).

The results of this risk analysis are presented in Table 9. The most striking variation in the probability of extinction was in the simulations of the model with a λ of 1, where only a large initial population (1,000 individuals) would ensure a null probability of extinction over 100 years. Such variation is exemplified by plotting the mean size of the population (excluding extinct ones) and mean probability of survival (the proportion of iterations in which the population is not extinct) over the entire 100-year timeframe (Figures 4 and 5, respectively).

It is clear from the results that in a stable population (λ = 1) the probability of extinction decreases steadily with the larger populations, with no risk (in 100 years) for those ≥ 1000 individuals. On the other hand, if the population is even only mildly increasing (λ ≤ 1.0.4) only very small populations (N_0 ≤ 25) are likely to be at any risk of extinction over the next 100 years. This is not an unexpected outcome as population size and trends in population size are known to be the best predictors of extinction risk (O'Grady et al., 2004), critical thresholds in these values would change depending on the biological characteristics of the species. This analysis demonstrates the common but complicated ways in which different processes can interact to put small populations of threatened wildlife at risk.

Table 9. *Key results of testing different λ values against different initial population sizes (N₀) — simulations were run 500 times over 100 years. rs = stochastic growth rate, SD(rs) = standard deviation of the stochastic growth rate, PE = probability of extinction, N(extant) = mean size of population after 100 years (excluding extinction events), SD(N(extant)) = standard deviation of the mean size of population (extant) after 100 years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction.*

λ	N₀	r_s	SD(r_s)	PE	N(extant)	SD(N(extant))	N	SD	Median TE	Mean TE
1.00	25	-0.0304	0.1577	0.8540	21.95	19.59	3.26	10.74	51	48.5
1.00	50	-0.0257	0.1344	0.6220	21.51	15.91	8.22	14.25	86	67.2
1.00	100	-0.0211	0.1104	0.3080	33.48	26.09	23.28	26.55	0	80.9
1.00	250	-0.0175	0.0810	0.0360	64.86	48.08	62.55	48.70	0	86.6
1.00	500	-0.0155	0.0669	0.0020	127.64	75.59	127.38	75.73	0	99.0
1.00	1000	-0.0150	0.0608	0.0000	256.20	145.35	256.20	145.35	0	0
1.02	25	-0.001	0.1140	0.298	65.79	53.09	46.25	53.65	0	56.4
1.02	50	0.0031	0.0892	0.064	114.87	88.11	107.53	89.75	0	70.4
1.02	100	0.0055	0.0682	0.002	218.44	142.2	218.01	142.38	0	98
1.02	250	0.0064	0.0553	0	536.51	272.34	536.51	272.34	0	0
1.02	500	0.0063	0.0516	0	1050.15	497.93	1050.15	497.93	0	0
1.02	1000	0.0068	0.0490	0	2147.96	894.91	2147.96	894.91	0	0
1.04	25	0.0248	0.0774	0.0260	442.48	335.83	430.98	338.83	0	54.4
1.04	50	0.0266	0.0577	0	854.91	490.92	854.91	490.92	0	0
1.04	100	0.0275	0.0487	0	1749.76	832.00	1749.76	832.00	0	0
1.04	250	0.0280	0.0434	0	3936.88	991.59	3936.88	991.59	0	0
1.04	500	0.0280	0.0415	0	4892.22	281.80	4892.22	281.80	0	0
1.04	1000	0.0281	0.0406	0	4946.19	106.94	4946.19	106.94	0	0
				0						0
1.07	25	0.0603	0.0476	0	4856.56	580.08	4856.56	580.08	0	0
1.07	50	0.0607	0.0386	0	4998.16	22.52	4998.16	22.52	0	0
1.07	100	0.0612	0.0339	0	4998.14	18.89	4998.14	18.89	0	0
1.07	250	0.0612	0.0314	0	4999.50	17.40	4999.50	17.40	0	0
1.07	500	0.0611	0.0304	0	4998.95	20.12	4998.95	20.12	0	0
1.07	1000	0.0614	0.0300	0	4998.50	20.37	4998.50	20.37	0	0
				0						0
1.1	25	0.0959	0.0318	0	5000.72	21.25	5000.72	21.25	0	0
1.1	50	0.0962	0.0261	0	5000.69	21.30	5000.69	21.30	0	0
1.1	100	0.0961	0.0226	0	5000.57	22.16	5000.57	22.16	0	0
1.1	250	0.0962	0.0207	0	4999.63	21.41	4999.63	21.41	0	0
1.1	500	0.0963	0.0201	0	4999.95	21.20	4999.95	21.20	0	0
1.1	1000	0.0963	0.0197	0	4999.55	20.66	4999.55	20.66	0	0
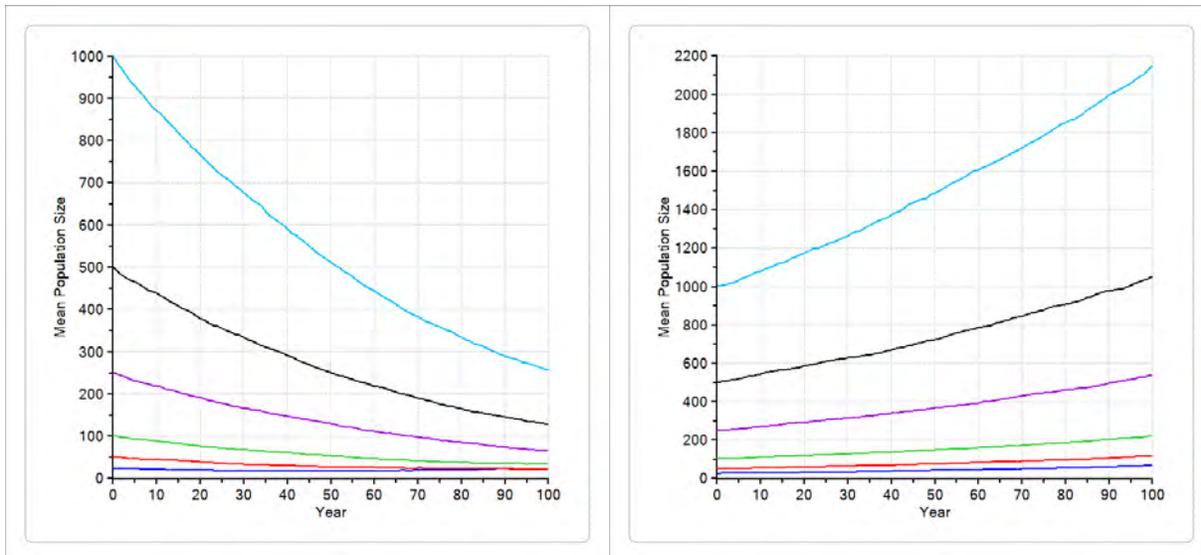
Figure 4. *The effects of initial population size on the mean size of the population (excluding extinct ones) with λ = 1 (left) and λ = 1.02 [dark blue = 25, red = 50, green = 100, purple = 250, black = 500, light blue = 1000] simulated for a 100 year (500 iterations).*
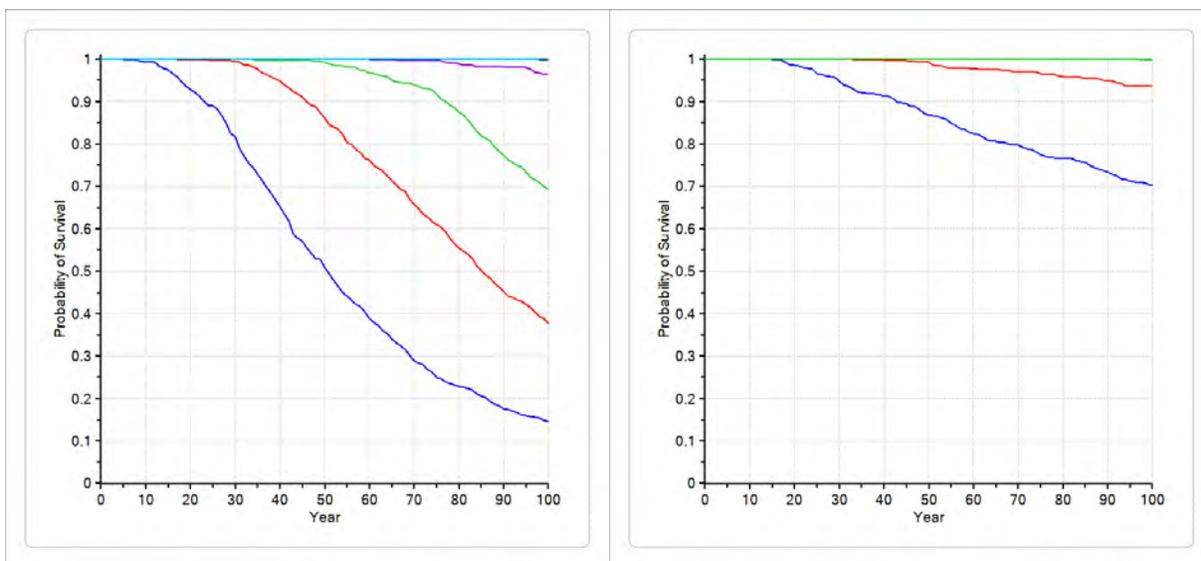
Figure 5. *The effects of initial population size on the probability of survival of the population (excluding extinct ones) with λ = 1 (left) and λ = 1.02 (right) simulated for 100 years (500 iterations) — dark blue = 25, red = 50, green = 100, purple = 250, black = 500.*

Figures 4 and 5 provide a more detailed look at the time course of extinction. These help to evaluate how the relative risk of extinction non-linearly changes over time frame. Note that the population's probability of survival (Figure 5) decreases non-linearly over time, as the population size typically declines as more extinctions occur over the time course of the computer simulation – even in the presence of a positive long-term stochastic growth rate. For example, a population initialized with 50 individuals has a 99% probability of survival in 25 years, but this decreases to 86 % in 50 years and 38% in 100 years. This is because demographic fluctuations destabilize populations over time increasing their risk of significant decline and possible extinction. When evaluating the results of

population viability analyses, it is important to project far enough into the future so that processes with longer time horizons have a chance to influence the course of the projection. This is particularly important for a species like the LTM, which has a potential maximum lifespan of ~30 years. An analysis period which was too short would fail to identify the longer-term trajectory and extinction risk on the population.

Phase 2: case scenarios

The LTM has a very large extent of occurrence but demographic information across the range can be scant and very variable (Hansen et al., 2022). More importantly, it is clear from the participative Threat Analysis exercise that different populations differ greatly in their size and in the threats they are facing (see *§ Threat Analysis Working Group Report*). Because of this, in consultation with a PVA working group, it was agreed that the best approach to explore the effects of threats on the species was by modelling particular case study scenarios. Such case study scenarios are "modelled on" real-world context but, due to the lack of precision in the estimate of many of the parameters, they are not necessarily a realistic depiction of those real-world situations. These case scenarios serve a diagnostic purpose, and they aim to highlight the potential impact of different threats under a selection of realistic conditions. Ultimately, results from these simulations provide useful insight to inform further modelling and would be a useful foundation upon which to draft a conservation management plan at a national or regional level. This would be best achieved by a participative process with the participation of all stakeholders e.g. please see the IUCN Species Conservation Planning Principles & Steps (CPSG, 2020).

Case Scenarios:

Six case scenarios were defined with the help of the organising team:

a. 'Large' population under harvest pressure (*e.g. Peninsular Malaysia, Thailand*)
b. 'Large' island population threatened by extreme weather events (*e.g. Nicobar Islands*)
c. 'Medium' population subject to disease outbreaks (*e.g. Padangtegal Monkey Forest, Bali*)
d. 'Medium' population subject to different types of harvest (*e.g. Lao PDR, Cambodia, Java*)
e. 'Small' island populations under harvest pressure, threatened by extreme weather events (*e.g. Karimunjawa Islands*)
f. 'Small' island populations threatened by extreme weather events (*e.g. Lasia Island, Maratua Island*)

Initial Population Size:

The terms 'large', 'medium' and 'small' are here used in relative terms and do not have a biological meaning. Initial population sizes were set to arbitrary values loosely inspired by real cases:

- 'large' = 2,000 individuals –   Thailand, Prey Lang in Cambodia

- 'medium' = 600 individuals – Padangtegal Monkey Forest (Bali) in 2010 (Brotcorne et al., 2015), Lao in PDR (Phiapalath & Hansen, 2023);

- 'small' = 200 individuals –   180 *M. f. tua* (Nuryati et al., 2022), 250 *M. f. lasiae* (Amey et al., 2022), 250 *M. f. karimondjawae* (Kristiawan et al., 2022);

Harvest

The word 'harvest' is henceforth used for the removal of individuals from a population. Depending on the area this may be for meat consumption, pet trade or export for the biomedical industry. From a population dynamics perspective, the final use of the individuals does not affect the potential consequences of such removal on the population, thus, the generic term 'harvest' will be used hereafter.

Depending on the geographical region and the final use of the yielded individuals, harvest can be implemented in different ways which are likely to have a different impact on the population. Harvest was modelled according to five different modalities (see § *Biological resource use* for mode detail on modalities, their use and distribution): (*a*) the targeting of adult males, (*b*) of adult females, (*c*) of 1- and 2-years old individuals, (*d*) the harvest of random individuals and (*e*) the removal of an entire group. For the first four modalities, the removal of 2.5%, 5% and 10% per year of the entire population was modelled, whereas a different approach was used for modality *d* (*see below*).

The **targeting of adult males, adult females** and **1- and 2-year-old individuals** was modelled by using the default functionality of *VORTEX* which allows to specify how many individuals are harvested from each of the age classes previously defined in the model. Individual and population state variables (*see* Lacy, Miller, and Traylor-Holzer 2021) were used to tally the total number of individuals for each age group at every time step of the simulation. Each year a desired fixed proportion of the total population (2.5%, 5% or 10%) was evenly harvested from the desired age class (adult males, or 1- and 2-year-old individuals).

The '*Catastrophe*' (see § *Catastrophes*) functionality was used to model the **random harvest** of a given proportion of the population. This allowed to yield the desired percentage of the population every year randomly across sexes and age classes.

To model the ***removal of an entire group*** a different approach was used. LTM group sizes tend to increase with the amount of resources available and they can vary over time by fission-fusion dynamics accordingly (Thierry, 2011). When modelling the harvest of groups two alternative default scenarios were created to simulate the removal of one or two groups per year from (1) an area of low quality (i.e. small group size = 40 individuals); and (b) high quality (i.e. large group size = 120 individuals). Group sizes where chosen arbitrarily based on available data from Padangtegal Monkey Forest, Bali, whereas the age composition of a 'typical' group was calculated from the same dataset by averaging (±SD) count results (8-10 groups across 11 years) i.e. infants = 16% ± 3%, juveniles 1-2 years = 14% ± 4%, juveniles 2-3 years = 18% ± 4%, subadult ♀♀ = 4% ± 1%, subadult ♂♂ = 7% ± 3%, adult ♀♀ = 32% ± 4%, and adult ♂♂ = 9% ± 3% (Brotcorne, 2014; Giraud, 2023; Giraud et al., 2021).

Catastrophes

Catastrophes are singular environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival. Natural catastrophes can be tornadoes, floods, droughts, diseases, or similar. These events are modelled in *VORTEX* by assigning an annual probability of occurrence and a pair of severity factors describing their impact of the catastrophe on mortality (across all age-sex classes) and the proportion of females successfully breeding in a given year. These factors range from 0 (maximum or absolute effect) to 1 (no effect), and are imposed

during the single year of the catastrophe, after which time the demographic rates rebound to their baseline values.

Extreme weather events

There is a concern that insular populations of LTM may be greatly affected by severe tropical storms and/or tsunamis (Sivakumar, 2010; Umapathy et al., 2003; Velankar et al., 2016). The effects of extreme weather events were modelled as 'catastrophes' in VORTEX (*see above*). The frequency of such events was set to a frequency of 48%. This was based on available meteorological data which show the incidence of category-5 tropical storms in SE Asia over the last 50 years (1972-2022) (Knapp et al., 2010). In some cases, a higher arbitrary frequency of 25% (~every 4 years) was tested to highlight the importance of this parameter. The only data available on the effects of an extreme event on LTM populations are from studies carried out in the Nicobar islands following a disastrous tsunami in 2004 (Velankar et al., 2016). In this instance, researchers, found no significant decrease in abundance but changes in the population structure and local abundance suggest an uneven effect on the populations. In order to follow a more systematic and consistent approach we tested for a 2.5%, 5% and 10% reduction in survival due to the event. This allows us to investigate and understand a broader spectrum of possible consequences, given that different populations are likely to react differently across the range.

Disease outbreaks

LTM's populations are susceptible to disease outbreaks which may significantly impact the population growth rate (Brotcorne et al., 2015; Phiapalath & Hansen, 2023). The risk of such outbreaks is often heightened when they live closest to human settlements and or at high densities (see § *Human intrusions & disturbance* and § *Residential & commercial development + Agriculture & aquaculture*). Data on the impact of outbreaks at a wild population level is scant. The additional mortality due to the disease outbreak was modelled on data collected in the wake of a 2022 *Streptococcus* outbreak in the Padangtegal Monkey Forest (Bali) population (Phiapalath & Hansen, 2023). The study showed that 3 out of 9 groups were impacted, infected groups showed an additional mortality rate ranging from 16% to 53%, and adult males and females were the most impacted, with mortality rates of 36% and 35% i.e. additional overall mortality of 1.9%-6.3% and 1.85%-6.16% for females and males, respectively (Phiapalath & Hansen, 2023). The frequency of outbreaks was set to 14 years (annual frequency = 7.14%) as it has been observed to be the average time interval between such events (Soedarmanto et al. 1996; Salasia et al. 2019; Patouillat et al. 2023). This was modelled by setting an additional 1.9% to 6.3% and 1.85% to 6.16% mortality for adult males and females, respectively. Given that the preliminary results showed a minimal effect of the above increase in mortality an additional model was set to have an additional 50% mortality for both adult males and females, in the attempt to simulate the potential effects of a particularly deadly and consequential outbreak.

Sensitivity analysis

Results from the running of the above models lead to the building of a series of additional models to investigate the relative sensitivity of LTM populations to increased mortality of specific age classes. All these models had an initial population of 25 individuals but each of them had a mortality rate 5% higher than the previous one (range = +5% - +75%). This sensitivity analysis was used to gauge the population sensitivity to the increase of adult female, adult male, juvenile female or juvenile male

mortality. For the sake of this analysis, 'juveniles' are here defined as individuals ≤ 1 year of age. Although initial tests were run for juveniles across sexes, LTM experts suggested that this analysis should distinguish between males and females to highlight the potential importance of sex over age. The analyses were run for both λ = 1.02 and λ = 1.06.

Carrying capacity

In each of the above simulations carrying capacity was arbitrarily set to the size of the next larger 'case study' population size and no more than 5,000 individuals i.e. 5,000 for the 'large' populations, 2,000 for the 'medium' and 600 for the 'small'.

Results

For clarity and brevity's sake, only a selection of the results from all modelled scenarios is reported here in the form of figures and tables.
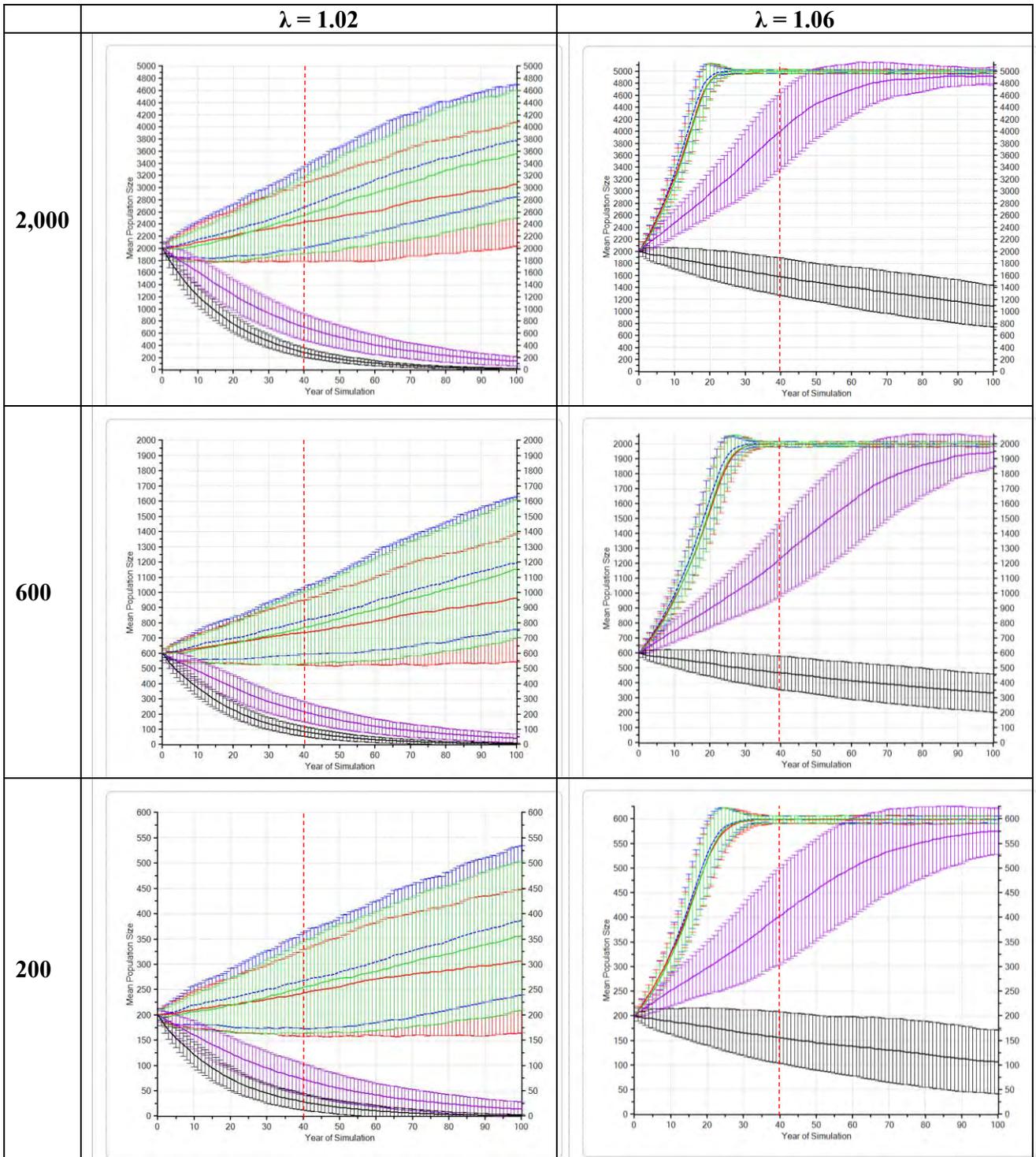
Effects of Harvest

Magnitude and methods

The baseline models exhibit different degrees of vulnerability to different magnitudes and methods of capture. While the effects of the removal of 1-2-year-old and adult males are relatively minor, the capture of adult females or random individuals has an increasingly greater impact, both in the short and the long term (Figure 6, table 11). Such effects are progressively more severe as the initial population size is set to increasingly smaller values (Table 11). It is important to note that, although some types of harvest may increase significantly the chances of a population being extirpated over 100 years, this may happen by means of a very gradual decline which may well be hard to detect with confidence in the field unless a consistent monitoring scheme is in place.

When looking at the removal of groups in their entirety, it is clear that this method has the potential to be very impactful. This is much more pronounced in a slow-growing population (Figure 7), although the effects are marked throughout the modelled scenarios. These simulations highlight more than ever the importance that the initial size has on the short- and long-term fate of the population (Figure 7, Table 12). This method of capture, depending on its scale, has the potential to cause sharp population declines that may cause the population to be extirpated as quickly as 10 years even in a large and fast-growing population e.g. yearly removal of two large groups from an initial population of 2,000 individuals with a λ of 1.06 (table 12).

A 100 years was deemed a suitable timescale to evaluate the long-term viability of the populations. However, conservation managers are often dealing with a much shorter timeframe when planning specific interventions. Moreover, generation length is often used by the IUCN to assess the level of threat of a species (e.g. criteria C1 and E; IUCN 2012). Because of this, a 40-year demarcation line has been added to all graphs showing the effect of harvest as this is compatible with the length of three generations (13.9 years × 3) currently accepted by the IUCN for this species (Pacifici et al., 2013).

Figure 6. *The effects of a 5% annual harvest with different capture methods on the mean population size over 100 years with an initial population of 2,000, 600 and 200 and λ = 1.02 and λ = 1.06 — error bars = SD, results from 500 iterations.* **Dashed blue line** *= baseline with no harvest,* **red line** *= 1-2 years old are targeted,* **green line** *= only adult males are captured,* **purple line** *= only adult females are taken, and* **black line** *= individuals are removed randomly across age classes. Dashed vertical red line = 40 years demarcation.*

Table 10. *Key results of simulating a 5% annual harvest with different capture methods over 100 years with an initial population of 2,000, 600 and 200 and a λ = 1.06 and λ = 1.02 — simulations were run 500 times. λ = finite growth rate, N_0 = initial population size, Harvest = method of capture, r_s = stochastic growth rate, $SD_{(rs)}$ = standard deviation of the stochastic growth rate, PE = probability of extinction, $N_{(extant)}$ = mean size of population after 100 years (excluding extinction events), $SD_{(N(extant))}$ = standard deviation of the mean size of population (extant) after 100 years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction*

Λ	N_0	Harvest	rs	SD(rs)	PE	$N_{(extant)}$	$SD_{(N(extant))}$	N	SD	Med. TE	Mean TE
1.02	2000	none	0.0069	0.048	0	3774.17	927.89	3774.17	927.89	0	0
1.02	2000	1-2-yrs	0.0039	0.0486	0	3057.63	1022.87	3057.63	1022.87	0	0
1.02	2000	ad ♂♂	0.0059	0.0492	0	3556.68	1048.42	3556.68	1048.42	0	0
1.02	2000	ad ♀♀	-0.0283	0.0541	0	136.3	76.03	136.3	76.03	0	0
1.02	2000	random	-0.0532	0.0905	0.196	17.05	11.52	13.88	12.18	0	91.9
1.02	600	none	0.0064	0.0507	0	1194.12	436.13	1194.12	436.13	0	0
1.02	600	1-2-yrs	0.0038	0.0515	0	964.82	423.59	964.82	423.59	0	0
1.02	600	ad ♂♂	0.0059	0.0515	0	1153.52	455.6	1153.52	455.6	0	0
1.02	600	ad ♀♀	-0.0299	0.0714	0.034	41.37	28.58	40.01	29.01	0	93.9
1.02	600	random	-0.0563	0.1164	0.724	10.37	7.15	3.07	5.9	89	82.3
1.02	200	none	0.0062	0.0579	0	386.52	147.59	386.52	147.59	0	0
1.02	200	1-2-yrs	0.0032	0.0588	0	306.09	141.9	306.09	141.9	0	0
1.02	200	ad ♂♂	0.0051	0.0589	0	356.07	147.76	356.07	147.76	0	0
1.02	200	ad ♀♀	-0.0319	0.1021	0.322	19.28	13.89	13.27	14.4	0	84.7
1.02	200	random	-0.0573	0.1353	0.932	8.44	4.88	0.65	2.47	69	67.4
1.06	2000	none	0.0502	0.0331	0	4992.95	30.92	4992.95	30.92	0	0
1.06	2000	1-2-yrs	0.0476	0.0332	0	4993.03	37.99	4993.03	37.99	0	0
1.06	2000	ad ♂♂	0.0495	0.0335	0	4993.57	30.9	4993.57	30.9	0	0
1.06	2000	ad ♀♀	0.0159	0.0323	0	4924.33	136.82	4924.33	136.82	0	0
1.06	2000	random	-0.0066	0.0349	0	1085.41	343.75	1085.41	343.75	0	0
1.06	600	none	0.0499	0.0341	0	1996.14	17.11	1996.14	17.11	0	0
1.06	600	1-2-yrs	0.0473	0.0342	0	1997.69	15.33	1997.69	15.33	0	0
1.06	600	ad ♂♂	0.0493	0.0349	0	1996.73	17.17	1996.73	17.17	0	0
1.06	600	ad ♀♀	0.016	0.0339	0	1945.33	102.4	1945.33	102.4	0	0
1.06	600	random	-0.0067	0.0412	0	331.64	128.96	331.64	128.96	0	0
1.06	200	none	0.0499	0.038	0	598.42	7.09	598.42	7.09	0	0
1.06	200	1-2-yrs	0.0474	0.0383	0	598.43	7.58	598.43	7.58	0	0
1.06	200	ad ♂♂	0.0495	0.0388	0	598.98	7.42	598.98	7.42	0	0
1.06	200	ad ♀♀	0.0158	0.0387	0	573.83	46.81	573.83	46.81	0	0
1.06	200	random	-0.0084	0.0583	0	106.41	64.85	106.41	64.85	0	0
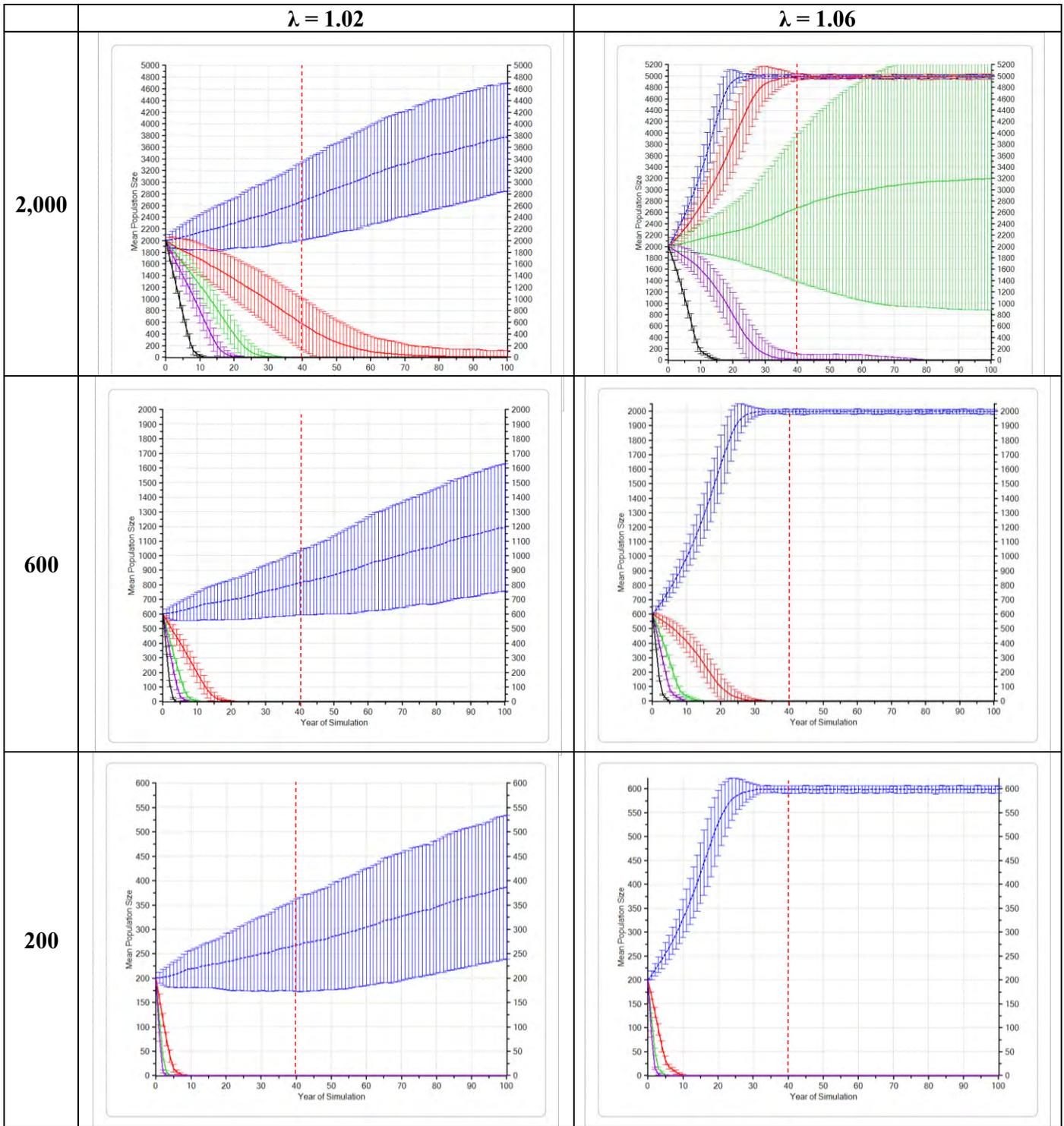
Figure 7. *The effects of the annual harvest of small(40 individuals) or large (120 individuals)groups on the mean population size over 100 years with an initial population of 2,000, 600 and 200 and λ = 1.02 and λ = 1.06 — error bars = SD, results from 500 iterations. **Dashed blue line** = baseline with no harvest, **red line** = removal of 1 small group of 40 individuals/year, **green line** = 2 small groups of 40 /year, **purple** = 1 large group of 120 / year; **black line** = removal of 2 large groups of 120 / year. Dashed vertical red line = 40 years demarcation.*

Table 11. *Key results of simulating the annual harvest of small(40 individuals) or large (120 individuals) groups on the mean population size over 100 years with an initial population or 2,000, 600 and 200 and λ = 1.02 and λ = 1.06 — simulations were run 500 times. λ = finite growth rate, N_0 = initial population size, Groups/year (size) = number of groups harvested per year (and their size), r_s = stochastic growth rate, $SD_{(rs)}$ = standard deviation of the stochastic growth rate, PE = probability of extinction, $N_{(extant)}$ = mean size of population after 100 years (excluding extinction events), $SD_{(N(extant))}$ = standard deviation of the mean size of population (extant) after 100 years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction*

λ	N_0	Groups/year (size)	rs	$SD_{(rs)}$	PE	$N_{(extant)}$	$SD_{(N(extant))}$	N	SD	Median TE	Mean TE
1.02	2000	none	0.0069	0.048	0	3774.17	927.89	3774.17	927.89	0	0
1.02	2000	1(40)	-0.0752	0.1289	0.996	1517.5	1284.81	6.11	111.81	52	53.6
1.02	2000	2(40)	-0.1454	0.179	1	0	0	0	0	25	25
1.02	2000	1(120)	-0.1956	0.1969	1	0	0	0	0	17	16.8
1.02	2000	2 (120)	-0.3359	0.2376	1	0	0	0	0	9	8.6
1.02	600	none	0.0064	0.0507	0	1194.12	436.13	1194.12	436.13	0	0
1.02	600	1(40)	-0.201	0.1861	1	0	0	0	0	15	15
1.02	600	2(40)	-0.3656	0.2392	1	0	0	0	0	8	7.7
1.02	600	1(120)	-0.4958	0.283	1	0	0	0	0	6	5.5
1.02	600	2 (120)	-0.8026	0.2838	1	0	0	0	0	3	3
1.02	200	none	0.0062	0.0579	0	386.52	147.59	386.52	147.59	0	0
1.02	200	1(40)	-0.466	0.2515	1	0	0	0	0	5	5.4
1.02	200	2(40)	-0.8261	0.2998	1	0	0	0	0	3	3
1.02	200	1(120)	-0.926	0.1111	1	0	0	0	0	2	2
1.06	2000	none	0.0502	0.0331	0	4992.95	30.92	4992.95	30.92	0	0
1.06	2000	1(40)	0.0387	0.0334	0	4987.1	44.42	4987.1	44.42	0	0
1.06	2000	2(40)	0.0043	0.0629	0.316	4667.18	963.43	3192.95	2312.59	0	64.8
1.06	2000	1(120)	-0.0986	0.128	1	0	0	0	0	26	27.1
1.06	2000	2 (120)	-0.232	0.1687	1	0	0	0	0	10	9.9
1.06	600	none	0.0499	0.0341	0	1996.14	17.11	1996.14	17.11	0	0
1.06	600	1(40)	-0.1108	0.1212	1	0	0	0	0	21	21.4
1.06	600	2(40)	-0.259	0.1698	1	0	0	0	0	9	8.7
1.06	600	1(120)	-0.3914	0.2084	1	0	0	0	0	6	6
1.06	600	2 (120)	-0.6757	0.2152	1	0	0	0	0	3	3
1.06	200	none	0.0499	0.038	0	598.42	7.09	598.42	7.09	0	0
1.06	200	1(40)	-0.3667	0.1915	1	0	0	0	0	6	5.9
1.06	200	2(40)	-0.6941	0.2234	1	0	0	0	0	3	3
1.06	200	1(120)	-0.8348	0.0788	1	0	0	0	0	2	2
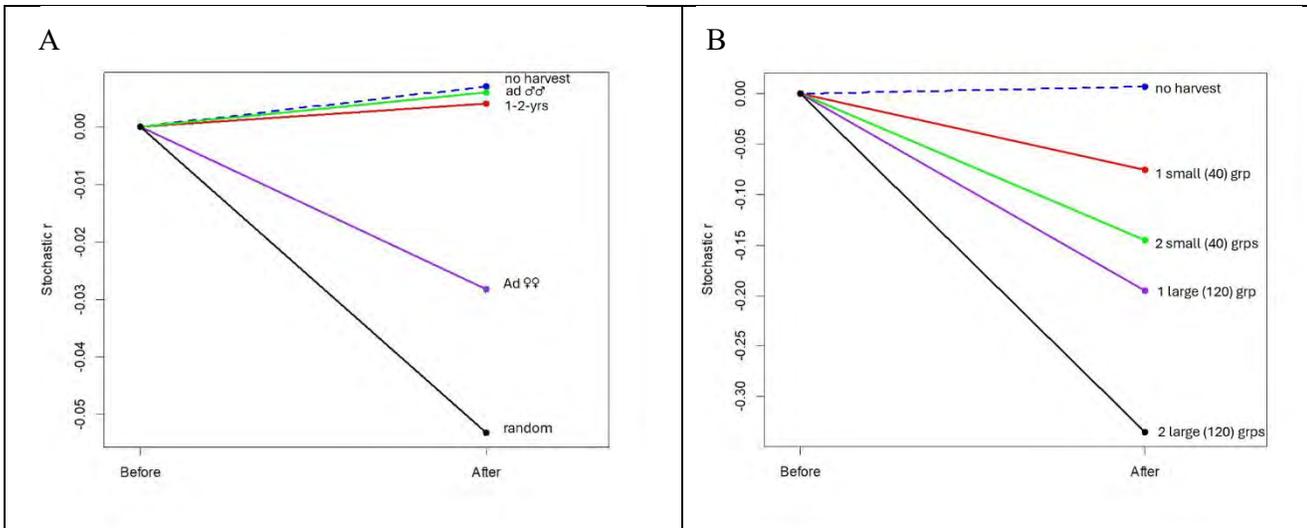
Figure 8. *Effect of **A.** different capture methods and **B.** different types of group capture methods on the stochastic r – results from the simulation of an initial population of 2,000 individuals with a and λ of 1.06 over a 100-year simulation period (500 iterations).*

Effects of extreme weather events

The simulation of extreme, sporadic but deadly events highlighted two key aspects. Firstly, those events which increase mortality non-discriminatorily across age classes are likely to have a more significant impact on the population trajectory in the long term even at reasonably low mortality rates (e.g. 2.5% per year, Figure 9, Table 13). Secondly, the frequency of such events will be a key factor in allowing the population to recover (or not) from the additional mortality. Although based on real data (see *§Phase 2: case scenarios: Extreme weather events*), the tested frequency of 48% (~ every two years) may be an overestimation of what is likely to happen on the ground. Strong tropical storms do indeed sweep the region with such frequency, but at an individual island/population level, the incidence may be much lower. A frequency of 25% (~ every four years) may be more realistic and yet results show that even with such a rate of recurrence the impact on the stochastic growth rate can be severe (Table 13). Ultimately, this highlights the additional level of vulnerability that populations may be subject to, particularly as they may inhabit smaller islands and coastal areas. This threat, no matter how infrequent it is likely to be compounded by other underlying environmental and anthropogenic pressures.
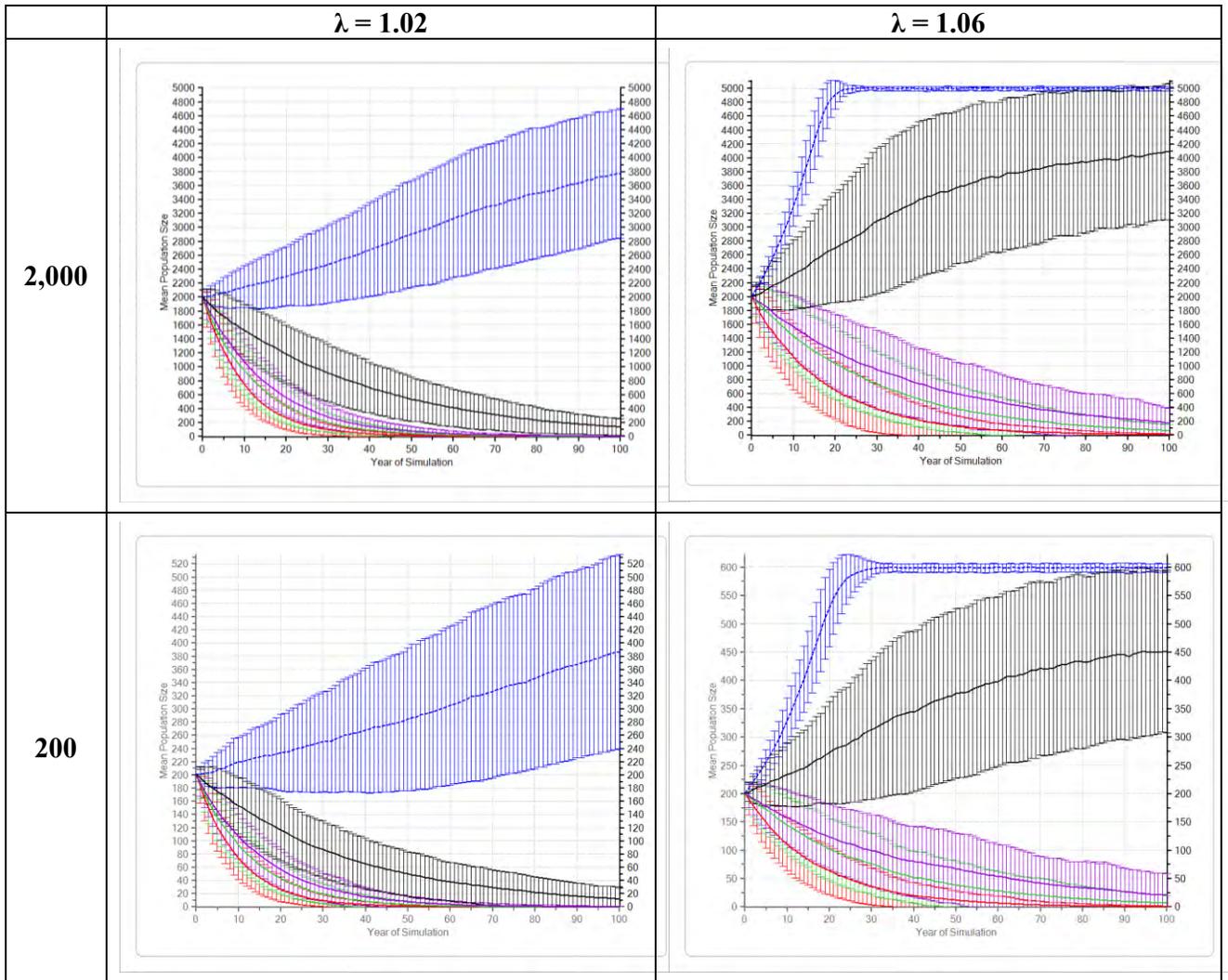
Figure 9. *The effects of a decrease of 2.5%, 5% and 10% in the annual survival due to a catastrophic event with a yearly 48% chance of happening and a decrease of 2.5% in the annual survival for an event with an annual frequency of 25%. Simulations were run 500 times over a 100-year period with an initial population of 2,000, and 200 and a λ = 1.02 and λ = 1.06 — error bars = SD.* ***Dashed blue line*** *= baseline,* ***red line*** *= -10% survival at 48% frequency,* ***green line*** *= -5% survival at 48% frequency;* ***purple line*** *= -2.5% survival at 48% frequency; and* ***black line*** *= -2.5% survival at 25% frequency.*

Table 12. *Key results of simulating a decrease of 2.5%, 5% and 10% in the annual survival due to a catastrophic event with a yearly 48% chance of happening and a decrease of 2.5% in the annual survival for an event with an annual frequency of 25%. Simulations were run 500 times over a 100-year period with an initial population of 2,000, and 200 and a λ = 1.02 and λ = 1.06. λ = finite growth rate, N0 = initial population size, Survival decrease = percentage decrease in yearly survival across age classes when the event strikes Frequency = yearly frequency of the catastrophic event, r_s = stochastic growth rate, SD(r_s) = standard deviation of the stochastic growth rate, PE = probability of extinction, N(extant) = mean size of population after 100 years (excluding extinction events), SD(N(extant)) = standard deviation of the mean size of population (extant) after 100 years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction*

λ	N_0	Survival decrease	Frequency	r_s	$SD_{(rs)}$	PE	$N_{(extant)}$	$SD_{(N(extant))}$	N	SD	Median TE	Mean TE
1.02	2000	none	-	0.0069	0.048	0	3774.17	927.89	3774.17	927.89	0	0
1.02	2000	10%	48%	-0.1118	0.179	0.998	8	0	0.03	0.39	56	57.7
1.02	2000	5%	48%	-0.0859	0.1568	0.94	6.03	3.79	0.43	1.71	74	73.4
1.02	2000	2.5%	48%	-0.0736	0.1444	0.764	8.81	6.3	2.28	4.78	86	79.9
1.02	2000	2.5%	25%	-0.0304	0.0984	0.006	135.19	117.19	134.38	117.29	0	89.7
1.02	200	none	-	0.0062	0.0579	0	386.52	147.59	386.52	147.59	0	0
1.02	200	10%	48%	-0.1115	0.1947	1	0	0	0	0	36	37.7
1.02	200	5%	48%	-0.088	0.1715	1	0	0	0	0.04	45	47
1.02	200	2.5%	48%	-0.0746	0.1596	0.99	5.8	5.76	0.08	0.79	53	55.1
1.02	200	2.5%	25%	-0.0353	0.1319	0.444	20.28	18.81	11.49	17.14	0	80.8
1.06	2000	none	-	0.0502	0.0331	0	4992.95	30.92	4992.95	30.92	0	0
1.06	2000	10%	48%	-0.0691	0.1663	0.67	17.1	20.49	5.89	14.16	91	80.7
1.06	2000	5%	48%	-0.0417	0.1275	0.076	70.49	90.93	65.18	89.35	0	88
1.06	2000	2.5%	48%	-0.0307	0.1115	0.018	177.6	213.13	174.41	212.51	0	88
1.06	2000	2.5%	25%	0.0128	0.087	0	4083.55	982.24	4083.55	982.24	0	0
1.06	200	none	-	0.0499	0.038	0	598.42	7.09	598.42	7.09	0	0
1.06	200	10%	48%	-0.0694	0.1816	0.974	5.77	4.46	0.2	1.19	58	58
1.06	200	5%	48%	-0.0445	0.1522	0.656	18.02	18.99	6.39	13.97	87	73.5
1.06	200	2.5%	48%	-0.032	0.1321	0.338	30.46	43.79	20.29	38.36	0	77.7
1.06	200	2.5%	25%	0.0122	0.0903	0	451.39	143.74	451.39	143.74	0	0

Effects of disease outbreaks

The first consideration to be made is about the data used for the simulation. The available information suggests that adult individuals are the most vulnerable to outbreaks. This is somehow surprising as infants and juveniles would be expected to be the most affected. Upon discussion with participants, there is currently no theory to explain this but it may be representative of a specific disease (*Streptococcus*). Moreover, available data show reasonably low levels of mortality even amongst those age classes that are affected. Because of this, it is not surprising that the populations display a reasonably high level of resilience to disease outbreaks in the simulations (Figure 10). Interestingly such high levels of tolerance are maintained even when significantly higher levels of mortality are hypothesised (e.g. 50% of all adults) with a λ of 1.06 (Figure 10, Table 13). A slow-growing population, on the other hand, is much less resilient to high levels of adult mortality and shows a declining mean population trajectory over a 100-year period. In many cases, the probability of the population being extirpated over the simulation period is still very low (Table 14), but the decline is inexorable. Once again this highlights, the case in which a population may be declining at a rate that may be difficult to detect in the wild without adequate monitoring schemes.

These results offer only a window into how an LTM population may be affected by disease outbreaks of different lethality. However, it is important to note that in the real world, effects are likely to be very much dependent on the disease, its virulence, its means of transmission, and the frequency of the outbreaks. Moreover, different populations will exhibit different levels of resistance depending on their genetic makeup and their epidemiological history.
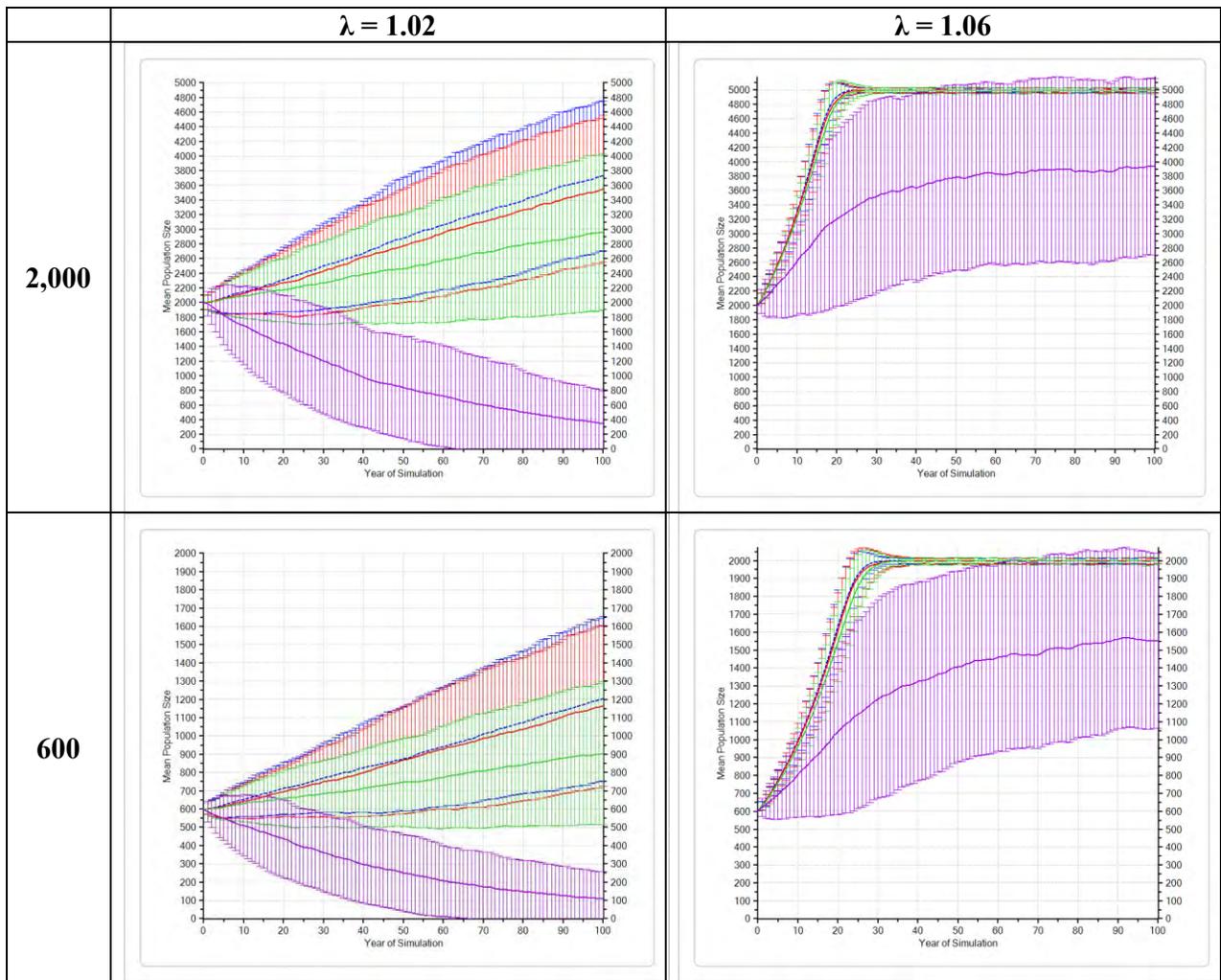
Figure 10. *The effects of a low-impact (**red line**), high-impact (**green line**) and very high-impact (**purple line**) disease outbreak with a 14-year frequency. Simulations were run 500 times over a 100-year period with an initial population of 2,000 and 600 and a λ = 1.02 and λ = 1.06 — error bars = SD. Blue dashed line = baseline with no disease outbreak*

Table 13. *Key results of simulating a low-impact (~2% additional adult mortality), high-impact (~6% additional adult mortality) and very high-impact (50% additional adult mortality) disease outbreak with a 14-year frequency. Simulations were run 500 times over a 100-year period with an initial population of 600 and a λ = 1.02 and λ = 1.06. . λ = finite growth rate, N0 = initial population size, Outbreak mortality = categories of additional mortality caused by the outbreak, r_s = stochastic growth rate, SD(rs) = standard deviation of the stochastic growth rate, PE = probability of extinction, N(extant) = mean size of population after 100 years (excluding extinction events), SD(N(extant)) = standard deviation of the mean size of population (extant) after 100 years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction*

λ	N_0	Outbreak mortality	r_s	SD(rs)	PE	N(extant)	SD(N(extant))	N	SD	Median TE	Mean TE
1.02	2000	none	0.0066	0.0481	0	3730.85	1023.73	3730.85	1023.73	0	0
1.02	2000	Low	0.0059	0.0483	0	3555.29	1001.89	3555.29	1001.89	0	0
1.02	2000	High	0.0034	0.0493	0	2962.39	1065.78	2962.39	1065.78	0	0
1.02	2000	Very High	-0.0247	0.1122	0.01	348.93	443.9	345.46	443.02	0	0
1.02	600	none	0.0064	0.0507	0	1204.65	449.88	1204.65	449.88	0	0
1.02	600	Low	0.0061	0.0508	0	1164.62	442.26	1164.62	442.26	0	0
1.02	600	High	0.0032	0.0521	0	904.03	390.57	904.03	390.57	0	0
1.02	600	Very High	-0.0258	0.1219	0.11	121	152.45	107.75	148.67	0	84.9
1.06	2000	none	0.0502	0.0331	0	4992.95	30.92	4992.95	30.92	0	0
1.06	2000	Low	0.0492	0.0332	0	4994.1	32.68	4994.1	32.68	0	0
1.06	2000	High	0.047	0.0343	0	4987.51	49.51	4987.51	49.51	0	0
1.06	2000	Very High	0.02	0.1005	0	3931.88	1229.49	3931.88	1229.49	0	0
1.06	600	none	0.0499	0.0341	0	1996.14	17.11	1996.14	17.11	0	0
1.06	600	Low	0.0491	0.0342	0	1998.32	14.15	1998.32	14.15	0	0
1.06	600	High	0.0472	0.0357	0	1996.44	17.52	1996.44	17.52	0	0
1.06	600	Very High	0.0203	0.1012	0	1551.68	488.13	1551.68	488.13	0	0

*Sensitivity analysis **–** adult and juvenile mortality rates*

The results of the sensitivity analysis highlight the importance of sex over age (Figures 11-12). At each consecutive 5% increase in female mortality (adult or juvenile), the mean projected population trajectory decreases substantially. This, in the case of a slow-growing population, can reverse the population's trend with just as little as 10% and 25% increased mortality in adult and juvenile females, respectively. On the other hand, LTM populations seem to be resilient both in the short- and long-term to a possible rise in male mortality, whether this involves juveniles or reproductively active adults (Figures 11-12) i.e. these results show that even a 75% increase is unlikely to affect the population trajectory significantly. These differences are clearly demonstrated by the stochastic r which, with a λ of 1.02, sees a decrease of 109% and 43% if adult female and juvenile female mortality rose by only 5%. In contrast, stochastic r would have virtually not change if it was an adult male or adult juvenile, respectively, to increase the same percentage.
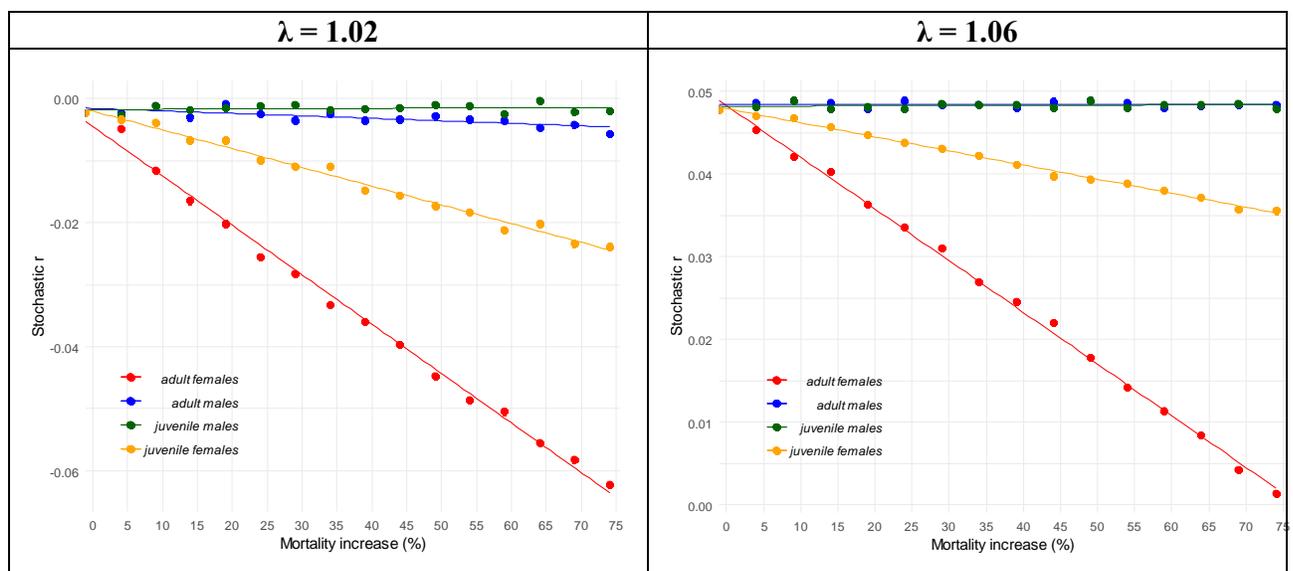
Figure 11. *Relationship between stochastic r and the incremental 5% increase in adult male (blue line), juvenile males (green line), juvenile females (yellow line) and adult female (red line) mortality (up to +75%) over a 100-year period on an initial population of 25 individuals with λ = 1.02 and λ = 1.06 – results of 500 iterations.*

Figure 12. (next page)*The effects of an incremental 5% increase in adult female, juvenile and adult male mortality (up to +75%) over a 100-year period on an initial population of 25 individuals with λ = 1.02 and λ = 1.06) – results of 500. Dashed blue line = baseline model, each colour = 5% increase.*

	λ = 1.02	λ = 1.06
Adult female mortality		
Juvenile female mortality		
Juvenile male mortality		
Adult male mortality		

Conclusions

The systematic semi-quantitative review of the threats affecting LTM populations and resulting population viability analysis reported here, provide useful evidence to establish a hierarchy amongst some of the different factors that can lead a population to decline and possibly go extinct. Although each real-life situation will have its own combination of natural anthropogenic variables, the systematic approach followed here allows prioritising conservation and management interventions based on the relative harmfulness of said threats. Such interventions may vary depending on the ultimate goal of the acting authority as well as their definition of 'viability'. For this reason, it is suggested the criteria embedded in the IUCN classification of threat categories are used as a yardstick to ensure the long-term viability of the species at different geographic scales (IUCN, 2012). Two results are most evident and they both have clear repercussions for the species conservation and its management.

Firstly, the presence and abundance of females in a population are key to its short- and long-term viability, with the 'importance' of adults overriding that of juveniles. It follows that any form of management intervention or natural event which negatively targets females is likely to threaten the viability of the population, more than similar interventions which target males (regardless of their class age). This was particularly apparent in the simulation of different methods of harvest, which willingly or not (e.g. random) target females (*§ Effects of Harvest*). This is also corroborated by a more systematic analysis of the effects of increased mortality of different ages classes and sexes (*§ Sensitivity Analysis*). Although understanding the relative importance of females may not be useful when dealing with the consequences of natural processes (e.g. diseases and natural catastrophes), it should be a crucial consideration when evaluating any conservation intervention. It is also important to stress that the effect of some threats may vary from one population to the next. For example, information on the impact of disease outbreaks was modelled on data from a population with a long history of proximity to humans, but less exposed populations (i.e. with a very different immunological history) may suffer a much greater toll.

Secondly, the models have emphasized the importance of the initial population size for its long-term viability. Information on LTM national and local abundance is scant and these results highlight the importance of filling this knowledge gap and implementing systematic population monitoring across its range, or at least of its main populations. Population estimates and trends in abundance are essential for the development of coherent conservation and management plans for wild animal species (Primack, 2006) and form the cornerstones of the IUCN Red List (IUCN, 2012). For species that are harvested from the wild and traded internationally, population monitoring is a legal requirement imposed by CITES (2023). Thus, population size is the most cost-effective data to collect on threatened species. Data on population size and trend, or indicators for them, should have priority in reports on the health of a nation's biological resources (O'Grady et al., 2004). The simulations undertaken here show clearly that, in some cases, although some interventions will cause a steady decline in the population, this may be slow and long-term, making it all the harder to detect with confidence in the field unless a consistent monitoring effort is undertaken.

Finally, it is important to remind the reader that the results presented in this report are to be interpreted with the necessary biological knowledge and care. The models are intended to be diagnostic tools and never to be adopted on their own as a justification for management decisions e.g. harvest quotas. For example, the results reveal that in some cases (e.g. harvesting one or two small groups in a population of 2,000 individuals with a λ of 1.06), the line between safe and ruinous management decisions is indeed very fine and managers should act based on the precautionary principle (Myers, 1993).

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Appendix I

Maximum lifespan

Although the participants agreed on a maximum lifespan of 23 years, due to the paucity of data from wild populations, it was hypothesised that this could be closer to ~30 years of age. To ascertain the relative importance of this parameter and its potential effects on the subsequent results, a number of diagnostic test were carried out.
Firstly, the simulation of the baseline model with a λ of 1 and an initial population of 25 and 250 were run both with a maximum lifespan of 23 and 30 (500 iterations for each simulation scenario). In both cases, the results didn't present any significant difference in the estimated number of years to extinction ($W = 89678$, $p = 0.35$ and $W = 71.5$, $p = 0.061$), nor the modelled population trajectory (Figure S1).

| $N_0 = 25$	$N_0 = 250$
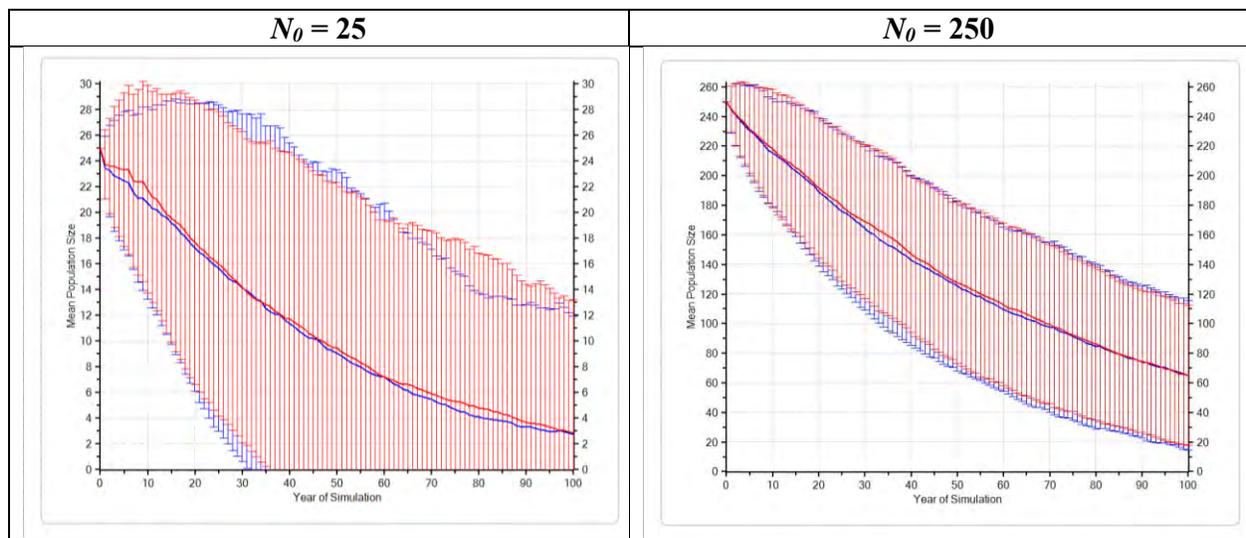
Figure S1. *Baseline model simulation with a maximum lifespan of 23 (blue line) and 30 years (red line). Simulations were run 500 times over a 100-year period with an initial population of 25 (left) and 250 (right) and a λ = 1.00— error bars = SD.*

Table 14. *Key results of simulating a 23 and a 30-year maximum lifespan. Simulations were run 500 times over a 100-year period with an initial population of 25 and 250 and a λ = 1.00. λ = finite growth rate, N_0 = initial population size, Outbreak mortality = categories of additional mortality caused by the outbreak, r_s = stochastic growth rate, SD(rs) = standard deviation of the stochastic growth rate, PE = probability of extinction, N(extant) = mean size of population after 100 years (excluding extinction events), SD(N(extant)) = standard deviation of the mean size of population (extant) after 100 years, N = mean size of population after 100 years (including extinction events), SD = standard deviation of the mean size of population after 100 years, Med. TE = median time to extinction, Mean TE = mean time to extinction*

N_0	Max lifespan	r_s	SD$_{(rs)}$	PE	N$_{(extant)}$	SD$_{(N(extant))}$	N	SD	Median TE	Mean TE
25	23	-0.0316	0.1584	0.874	21.22	16.86	2.73	9.21	48	47.5
25	23	-0.03	0.1572	0.852	19.01	20.5	2.86	10.34	53	48.7
250	30	-0.0168	0.0804	0.028	66.75	49.89	64.91	50.37	0	85.1
250	30	-0.0167	0.0801	0.034	67.25	46.64	64.99	47.39	0	91.2

Secondly, the potential effects of maximum lifespan on the modelled scenario were also tested when the population was under strain from a specific threat. To achieve this a particularly 'taxing' scenario was selected i.e. an initial population of 200 individuals with a λ of 1.02 and a yearly harvest of adult females only amounting to 5% of the population (*§Effects of Harvest, Magnitude and methods*). Each scenario was simulated 500 times. Again, the longer maximum age span made negligible difference to medium- to long-term estimated mean trajectory of the population (Figure S2) and there was no significant difference in the estimated number of years to extinction (W = 16170, p = 0.12).
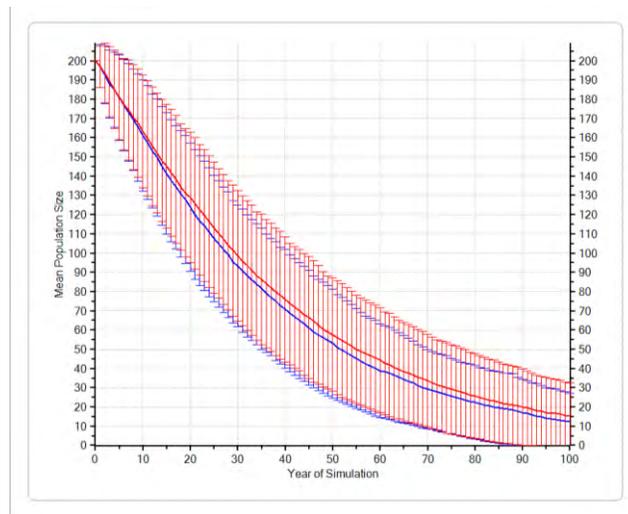
Figure S2. *Simulation of the effects of a 5% annual harvest of adult females only on the mean population size over 100 years with an initial population of 200 and λ = 1.02 — error bars = SD, results from 500 iterations. Blue line – maximum lifespan = 23 years, red line - maximum lifespan = 30 years*