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Refining the matrix population model of Balinese macaques under birth control: current outcomes and future projections

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Résumé

Amélioration du modèle matriciel d'une population de macaques balinais sous contrôle de naissance: premiers résultats et futures projections

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Promoteurs: Pr. Nicolas Schtickzelle et Dr. Fany Brotcorne

Suite à la déstructuration de l'environnement notamment via l'urbanisation, l'expansion agricole et la déforestation, le nombre de zones de contact entre l'Homme et les animaux sauvages ne cesse d'augmenter. Plus particulièrement dans les zones tropicales, beaucoup de populations de primates vivent en milieux anthropiques et en « co-écologie » avec l'humain, les forçant à s'adapter à un nouvel environnement. La population de macaques à longue-queue (*Macaca fascicularis*) de la Forêt des Singes d'Ubud à Bali (Indonésie) vit dans ce type d'interface, où elle est quotidiennement approvisionnée et n'a plus de prédateur. En plus de leur étonnante capacité d'adaptation à l'environnement, les singes d'Ubud voient dans ces conditions leur survie et leur fertilité augmenter alors que leur mortalité diminue, dans un habitat toujours plus restreint. Ces différents facteurs conduisent à un phénomène de surpopulation mettant en péril autant les communautés locales que les macaques. En 2017, des analyses de viabilité de la population (PVA) incluant un modèle matriciel de population ont été réalisées dans le but de calibrer un programme de stérilisation (par tubectomie des femelles) destiné à contrôler l'expansion de la population en la maintenant à l'équilibre et ainsi atténuer les risques liés au conflit macaque-humain. Différentes campagnes de stérilisation ont donc été réalisées entre 2017 et 2019 afin d'atteindre l'objectif du taux de stérilisation fixé par le modèle matriciel (52% des femelles adultes). Ce mémoire a pour but d'affiner le modèle matriciel de la population établi en 2017 en : (i) incluant les nouvelles données collectées entre 2017 et 2020, (ii) ajoutant les données liées aux stérilisations et des paramètres comportementaux des femelles (rang hiérarchique et expérience maternelle) supposés influencer leur succès reproducteur et donc la démographie de la population. Le but était de construire de nouvelles projections de la démographie de la population selon différents scénarios (i.e. présence d'épidémies). Un modèle matriciel plus complet a donc été construit à partir du précédent modèle, dans un premier temps de façon théorique en incluant davantage de paramètres (biologie de l'espèce, réalité de terrain/données,...) et ensuite testé via des analyses statistiques basées sur le critère d'information d'Akaike (AIC) à l'aide du software SAS®. Le modèle final sélectionné n'est pas beaucoup plus compliqué que le modèle précédent puisque seules les données liées aux stérilisations ont pu être incluses. Les projections de la population sur une période de 25 ans indiquent que d'autres efforts réguliers de stérilisation devront être fournis afin de maintenir la population à l'équilibre et ainsi atténuer les problèmes liés au phénomène de surpopulation.

Mots-clés : interface humain-primate, macaque, surpopulation, contrôle de population, stérilisation, modèle matriciel de population, PVA, projections.

Abstract

Refining the matrix population model of Balinese macaques under birth control: current outcomes and future projections

Fanny de Thier Nagelmackers, Academic year 2020-2021

Advisors: Pr. Nicolas Schtickzelle and Dr. Fany Brotcorne

Following environment disturbances such as urbanisation, agriculture expansion and deforestation, the number of contact zones between humans and wildlife is constantly increasing. Particularly in tropical zones, many primate populations live in anthropogenic habitats under "co-ecologies" with humans, which forces them to adapt to novel environments. The long-tailed macaque (*Macaca fascicularis*) population of the Ubud Monkey Forest in Bali (Indonesia) coexists with humans in such an interface, where it is daily provisioned and without any predation pressure. In addition to their noteworthy capacity of adaptation to environmental changes, under such conditions, Ubud macaques have higher survival chances and fertility and lower mortality rates, in a decreasing habitat area. As a result, the population faces a phenomenon of overcrowding, endangering both local communities and monkeys. In 2017, population viability analyses (PVA) including a matrix population model were developed in order to calibrate a sterilisation program (via female tubectomy). The latter aimed at controlling the population growth by holding it back at the equilibrium and therefore mitigating the risks linked to the human-macaque conflicts. Several sterilisation campaigns took place between 2017 and 2019 to reach the initial sterilisation rate fixed by the matrix population model (i.e. 52% of reproductive females). This master's thesis aims at refining the matrix population model established in 2017 by: (i) including the updated data collected between 2017 and 2020, (ii) adding the data related to sterilisations and some behavioural parameters of females (hierarchical rank and maternal experience) supposed to impact their reproductive success and therefore the population demography. The aim was to build new projections of the population trends under several scenarios (i.e. epidemic outbreaks). An improved matrix model was built based on the previous one, first theoretically, by including further parameters (species biology, data and field reality, ...) and finally through statistical analyses based on the Akaike information criterion (AIC) using SAS® software. The final model selected is not much more complex than the previous one since only the data related to the sterilisations was inserted. Projections of the population trends over 25 years indicate that further regular sterilisation efforts should be undertaken to manage the population and maintain it at the equilibrium, thereby mitigating the problems related to the overcrowding situation.

Key words : human-primate interface, macaque, overcrowding, population management, sterilisation, matrix population model, PVA, projections.

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♫ «*And tell me what to believe, and tell me what to deny. And whisper into my ear till everything dark turns bright* » ♫

TERIMA KASIH ♥



«*You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what kind of difference you want to make.* »
Jane Goodall

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INTRODUCTION

I Global context

Since the dawn of time the human primate, *Homo sapiens sapiens*, has been inhabiting nature, sharing space and resources with organisms. However, with the dramatic human population growth, sharing has become more and more difficult. After a steady rise over the past 10,000 years, the global human population suddenly grew from the 19th century and then faced a historical growth during the 20th century (Bongaarts, 2009; Chakraborty et al., 2013). In fact, the population has more than doubled since 1950 and in January 2020, 7.8 billion people were present on Earth (*FAOSTAT* 2019).

Together with population growth, demand for resources has augmented and human activity has had dire consequences on nature. Due to pollution, hunting, harvesting and the reshaping of land surfaces through urbanisation and land-use conversion, ecosystems has become severely disturbed (Crutzen, 2006; Lewis et al., 2015). All these issues, in particular land-use conversion, influence non-human life since it reduces the surface and resources available to millions of other organisms on the globe, bringing numerous species to extinction (Laurance et al., 2014). This induces scientists to talk about a biodiversity crisis and the likelihood of the sixth mass extinction in Earth's history. The latter phenomena serve as arguments commonly used by scientists to argue the existence of a new geological epoch, called the Anthropocene, given the importance and profundity of the human-induced changes of the environment and because they may be visible geologically for the next millions of years (Crutzen, 2006; Lewis et al., 2015). This definition is still controversial but can clearly show the importance of human impacts on the environment.

Nowadays, approximately 70% of worldwide terrestrial ecosystems are influenced by human doings. Among these human issues with nature, an important one is the Human-Induced Rapid Environmental Change (HIREC), leading to behavioural and population adaptations in other animal species. Different kinds of HIREC are described: habitat loss and fragmentation, introduction and expansion of exotic species, harvesting, spread of pollutants and climate change (Sih, Ferrari, et al., 2011). In this topic, I will focus on the impacts of habitat disturbances in the tropics and later describe the different types of scenarios observed for the non-human primates.

Tropical nature is seriously impacted by habitat loss and fragmentation. Regarding the importance of Earth's biological diversity supported by tropical ecosystems (many biodiversity hotspots are found in the tropics (Myers et al., 2000)), the threats to biodiversity are alarming. A major issue is the encroachment of human settlements and activities on tropical forests. Especially agricultural expansion is responsible for important rates of deforestation (Isabirye-Basuta et al., 2008; Laurance, 2007; Laurance et al., 2014). According to Laurance et al. (2014) "*the tropical evergreen and deciduous forests originally spanned 17 million km^2 globally and have now declined to 11 million km^2*". They even predict that forests will not stop declining this century, since 11–36% of existing forests in 2000 are predicted to disappear by 2050. Also, the majority of the remaining forests are severely altered or fragmented by anthropogenic influence (Laurance et al., 2014). In Indonesia for example, the mean deforestation rate reached 2 million ha/year between 1995 and 2000. This means that, over five years, Indonesia lost 24.1% of its forest cover, mainly due to logging and palm-oil plantation/cultivation (Butler, 2013).

Following deforestation, many wildlife species are constrained to adapt to a novel environment (Isabirye-Basuta et al., 2008; Sih, Trimmer, et al., 2016). Within the animal kingdom, non-human primate (hereafter referred to as primates) populations are particularly affected by the HIREC of habitat disturbances. As a consequence, about 60% of primate species (278 species out of the 504 described species) are threatened with extinction (Estrada et al., 2017; Galán-Acedo et al., 2019). Having a strong history of sympatry with *H. sapiens* populations which burgeon constantly, primate habitats have been intensively invaded (Daspit, 2006; Riley, 2007). The number of contact zones and overlapping areas between primates and humans consequently augmented and they are still increasing. In these areas, species do not only share space, they also coexist under the same ecological conditions, i.e. co-ecologies. Experts even determined the term of "interface", that is, every kind of interaction happening between humans and primates in their common environment, ultimately leading to competition for land-use and resources, and major species adaptations (Daspit, 2006; Galán-Acedo et al., 2019; Sih, Ferrari, et al., 2011; Sih, Trimmer, et al., 2016).

Animals facing HIREC pressures have to exhibit adaptive responses or perish. Generally, some animals can face the novel situation by adapting immediately and favourably, while other animals will tend towards a maladaptive evolution, often causing population decline (Isabirye-Basuta et al., 2008; Robertson et al., 2013; Sih, 2013; Sih, Ferrari, et al., 2011). Two major factors, which depend on the species fitness advantages and ecological traits, can influence the adaptative response. First, if the novel human-influenced environment is not too different from the one the organisms have seen in the past, they can adapt more properly to the new conditions (Galán-Acedo et al., 2019; Sih, 2013; Sih, Ferrari, et al., 2011; Sih, Trimmer, et al., 2016). Secondly, generalist species, which can use high ranges of available resources (*EEA Glossary* 1998; Sha et al., 2013), may be more able to face environmental changes than specialists (Robertson et al., 2013; Sih, 2013; Sih, Ferrari, et al., 2011). Galán-Acedo et al. reported in 2019 that 17% of worldwide primate species feed actively in human-altered landscapes and suggested that many of them are generalists. Such generalists are for example the Cercopithecidae family, including the genus *Macaca*. As these animals are more tolerant to the human-modified environments, they respond less negatively to anthropic impacts and are sometimes favoured by novel conditions (Galán-Acedo et al., 2019; Sih, Ferrari, et al., 2011; Sih, Trimmer, et al., 2016).

Therefore, even if extreme cases of primate species of the genus *Macaca* taking completely opposite directions under environmental interface pressures – some species decline while populations from others expand successfully – have been documented in the literature, many macaques are more likely to thrive under HIREC pressure. Indeed, some of them present favourable traits (see below) which offer them the ability of coping with the HIREC (Daspit, 2006; Galán-Acedo et al., 2019; Radhakrishna et al., 2012; Sih, 2013; Sih, Ferrari, et al., 2011). In turn, some macaque populations will be extremely successful and expand, sometimes attaining high density population (Richard et al., 1989).

Nevertheless, species able to succeed under HIREC pressure represent only a minority. The majority of species, including generalists, are indeed declining under. The ability to face HIREC is actually a local phenomenon, usually at the population level. For a given species globally threatened in human-modified environments, it is possible to find some populations with dramatic growth. This is usually due to habitat constriction or environmental conditions forcing them to congregate in one place, often small (Brotcorne, 2014; Sih, 2013; Sih, Trimmer, et al., 2016). For instance, the polar bear, *Ursus maritimus*, is a species assessed as *Vulnerable* in the International Union for Conservation of Nature (IUCN) red list (Regehr et al., 2016; Wiig et al., 2015) due to climate change and ice melting among other reasons. Most of polar bear populations are threatened (Amstrup et al., 2013; Obbard et al., 2010; Rode et al., 2014; Stirling et al., 2012) but few populations actually show growth. Indeed, following ice breaking and melting, bears migrate south to feed. They begin to inhabit cities or villages in some areas, as it has been seen in 2019 in Ryrkaypiy town, Russia ("Ryrkaypiy" 2019) or in the Hudson Bay, Canada (Peacock et al., 2010). These bears are sharing space with humans and regarding the abundance of human-derived food, some populations can increase significantly in size (Crockford, 2015; Peacock et al., 2010).

Across the tropics (mainly in Africa and Asia), sometimes associated with situations of overcrowding, some macaque populations become a pest in shared areas. The most famous case is probably the rhesus macaque, *M. mulatta*, invading and damaging local crops in India (Saraswat et al., 2015). Thus, many cases of conflicts between humans and monkeys in shared areas – especially in rural habitats and tourist sites or cities – are reported. Conflicts have consequences on macaques themselves, humans and their relationship. Taken as a whole, interactions between primates (especially macaques and baboons) and people within a co-ecology can put both humans and primates at risk (Devaux et al., 2019; Fuentes, 2012; Hill, 2005; Hill and Wallace, 2012; Lee, 2010; Lee and Priston, 2005; Radhakrishna et al., 2012; Riley, 2007).

In the scenario where populations or species are declining, scientists usually perform the population viability analysis (PVA). PVA is a collection of methods that gathers biological, ecological, demographic and statistical data about a population from a given species, with the joint use of computational simulations, and aims at estimating the likelihood of this population to become extinct in a specific period of time. It is built on a case-by-case basis: a PVA for a population in particular conditions will be different from the PVA of another population of the same species in other conditions. PVA allows the estimation of different management options for a population or species, helping to implement the ideal conservation programs in order to manage and restore the population (Akçakaya et al., 2000; Beissinger et al., 1998; Boyce, 1992; Keedwell, 2004; Reed, Mills, et al., 2002; Reed, Murphy, et al., 1998).

Regarding the conflictual situations mentioned above, population control is sometimes necessary to mitigate the uncontrolled growth. The situation of overcrowded populations becoming pests/nuisances follows basic ecological concepts similar with those of declining populations. To control such populations, we can thereby apply (modified) management programs. In fact, via the same tools as in conservation biology such as the PVA and different models, we can assess and predict the population trends (Reed, Mills, et al., 2002; Reed, Murphy, et al., 1998). This master's thesis focuses on one management method (i.e. birth control) in the specific case of a macaque (*Macaca fascicularis*) high-density population in Bali, Indonesia. We aim at refining a matrix population model to assess the efficacy of a birth control program (Cloutier et al., 2018).

II Population control: key concepts

II.1 Why using models in population biology?

Demographic population models are a mathematical expression aimed at understanding, explaining, and predicting the dynamics of a population, using different tools and parameters (Hastings, 2013). In the case of population growth, models help to manage the population, by illustrating, representing and predicting the population trends under different conditions and scenarios. These models are included in the PVA method and are based on basic concepts in ecology and on the specific parameters of the studied population. The purpose of this section is to clarify basic concepts of population biology in order to understand the problematic and objectives of the thesis.

It is important to keep in mind that "*populations are dynamic entities, that fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species*" (OpenStax, 2020). According to Chavas (2015), population dynamics refer to complex processes determining birth and death rates, immigration and emigration, the effects of age structure, and the influence of many biological and environmental factors affecting the survival and reproduction of individuals, and hence of their population. Modelling demographic dynamics, by formulating predictions and suggesting suitable solutions to demographic problems, is an essential aspect of the current conservation efforts. Not only interesting for the conservation of endangered species, it is increasingly used to manage pest species and mitigate overcrowding situations (Chavas, 2015; Townsend et al., 2003).

II.2 Population size, population density and demography

The population size (N) refers to the number of individuals in a given population, while the population density concerns the number of individuals per unit area or volume. These two measures are of primary concern to know whether a population control or a conservation program should be implemented or not. By using the population size and density, and statistical tools, we can study the demography of the population

over time. For instance, the changes in population size and structure can be studied. Thus, demographic studies allow to understand previous variations of the population and to predict its changes in the future (OpenStax, 2020; Townsend et al., 2003).

II.3 The carrying capacity of the environment

Usually, the demography of a population follows a standard trend (Figure 1). Initially, the number of individuals increases exponentially due to suitable conditions, such as abundance of resources and low predator pressure. However, the population cannot grow indefinitely (Hastings, 2013; OpenStax, 2020; Townsend et al., 2003). Environmental pressure will impose population to stabilise. The population will reach a plateau, the so called carrying capacity (K) of the environment, defined as "*the maximum density of a species that the environment can support on a sustained basis without being degraded*" (National-Research-Council, 1981). In other words, the population size will stop augmenting due to a lack of resources regarding the excessive number of individuals (OpenStax, 2020; Townsend et al., 2003). Overcrowding is actually closely related to the carrying capacity of the environment since the population size should not exceed the threshold (K) above which the environment could not provide enough resources, and where the population would harm the upper ecosystem. Thus, a population should be considered as overcrowded when it reaches the plateau level of K, corresponding to the point where resources become limited to support the population size (Townsend et al., 2003).

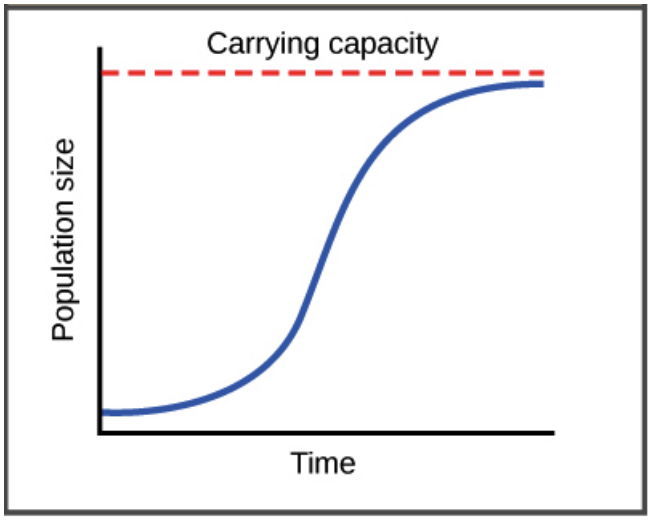


Figure 1: Graph of the logistic growth of a population. The vertical axis represents the number of individuals within a population while the X axis refers to the time, the blue line represents the logistic growth curve. ©Khan Academy

II.4 Life-history traits

To model population demography and dynamics, an essential point is the focus on the individuals' traits within a population. Bonner (1965) is the founder of the *life-history theory*, which is a field of evolutionary ecology (Alonzo et al., 2008). The theory is aimed at explaining the ways evolution and natural selection formed the organisms and at predicting the future trends of natural selection. Instead of describing organisms only by their adult state, we consider their entire life cycle. More precisely, life-history theory "*seeks to explain the diversity of tactics through which different organisms achieve evolutionary persistence and increase, why the tempo and mode of reproduction can vary so much across taxa, and why life cycles vary from species to species*" (Jones, 2011). Here, evolutionary persistence (or success) is based on two demographic phenomena: the survival of infants allowing them to reach the age of sexual maturity and the successful reproduction (Alonzo et al., 2008; Charnov, 1991; Jones, 2011; Stearns, 1976; Townsend et al., 2003).

The life-history traits are fitness components (and their interaction) of the individuals. They are naturally selected through evolution under environmental pressure and are transmitted across generations. Thus, they participate to the evolution and ecology of the species and populations. Among these traits are to be found the age-, stage- or size-specific reproductive effort, e.g. sexual maturity or first reproduction age; age-, stage- or size-specific rates of survival; lifespan, mortality, migration, ... (Stearns, 1976; Townsend et al., 2003). All these traits influence population trends since they determine the duration individuals stay in a population because they have direct effects on the resources, reproduction and population health or status (OpenStax, 2020; Townsend et al., 2003).

In demographic studies, two life-history traits are particularly important: the mortality rate and the birth rate. The population dynamics depends on how these two rates are balanced. We generally define a population as stable if its birth and mortality rates are at an equilibrium. In this case, the population remains stable, without any growth. However, the population size augments dramatically with a decrease of the death rate together with an increase of the birth rate (Brotcorne, 2014; Cloutier et al., 2018; National-Research-Council, 1981; OpenStax, 2020; Townsend et al., 2003).

Generally speaking, primates show a K-selected species pattern. K-selected species fluctuate close to the carrying capacity of their environment. Contrarily to the r-selected species where the dynamics are governed by the maximum reproduction capacity and where populations present high growth rates (OpenStax, 2020; Townsend et al., 2003). Therefore, in the K-selected pattern, as for primates, the number of offspring is low (usually one individual for each gestation) and parental care favours the offspring survival. Infancy period is slow and after reaching sexual maturity the growth stops to let the reproductive period begin. Primates finally die when they become elderly. If we compare them to other big mammals, primates have a slow life history. In fact, they mature late in their development, have a long lifespan and show a low fertility. Furthermore, they are species adapted to stable and predictable environments (Charnov, 1991; Harvey et al., 1985; Jones, 2011; National-Research-Council, 1981; OpenStax, 2020).

II.5 Population regulation

The logistic model of population growth (Figure 1) is a simplified version of what happens truly for a population. The model assumes that the carrying capacity is constant and without any variation. Yet, the carrying capacity shows spatio-temporal variations according to various conditions. Furthermore, factors such as seasonality, climate, resource availability or stochastic phenomena change the carrying capacity threshold. The simplified model does not consider either of the different interactions present inside a population, such as competition for space and resources, predation, etc. Yet population size is regulated naturally through two main types of factors: the density-independent and the density-dependent factors (Hastings, 2013; OpenStax, 2020; Townsend et al., 2003).

(a) *The density-independent factors:*

These factors impact the death rate of a population despite its density. In other words, "*in a density-independent population growth, the birth and death rates per individual do not depend on the population size*" (Hastings, 2013). Such factors depend on nature stochasticity and are mainly abiotic, including natural disasters, climate or pollution. The probability of death or survival of given individuals from a population therefore only relies on the impacts of the factors and not on the density of the entire population. Also, K is determined by the resource undergoing limitation. For example, an environment may offer enough food for a population but not enough space (the limited resource), hence preventing individuals from reproduction (Boyce, 1992; OpenStax, 2020; Townsend et al., 2003).

(b) *The density-dependent factors:*

Such factors are mainly biotic and are intrinsically related to the density of the population, since they intensify as the population density increases. The population size will be regulated "by itself" through predators, competition, diseases and parasites, territoriality or cannibalism, infanticide, lack of food supplies, etc. (Boyce, 1992; Hastings, 2013; National-Research-Council, 1981; OpenStax, 2020; Townsend et al., 2003).

(c) *Interaction between density-dependent and -independent factors:*

In reality, the two types of factors are not well divided and do not act separately. They actually interact and in turn, regulate population size. For instance, if a highly dense population faces a natural disaster (density-independent factor) regulating the population size, the remaining population will recover in a better way through density-dependent factors (Hastings, 2013; OpenStax, 2020; Townsend et al., 2003).

II.6 Age- and stage-structured populations

Populations follow a structure related to individual ages or stages. By these means, we can describe a population given its age or stage structure. The age structure of a population refers to the proportions of individuals that fit into the different age classes, which may vary in time as individuals get older. Besides, within a given population, different stages can be described. These stages are defined on several criteria such as individual phenology or behaviour. The stages do not vary automatically within time, since an individual can remain in a stage during several time-steps. The use of stages rather than age classes is convenient when the different ages of the studied individuals are impossible to determine. Knowing the parameters related to the different stages, such as the vital rates (i.e. the probability of individuals going from a stage to another), it is easier to understand the population and thus to predict its growth trends. Indeed, the allocation of individuals into the different stages reflects the turnover of a population (Alberts et al., 2003; Boyce, 1992; Caswell, 2001; Manly, 1990; National-Research-Council, 1981; OpenStax, 2020; Townsend et al., 2003).

II.7 Life cycle: the link between individuals and population

The life cycle is a unit aimed at describing an individual's standard life through different parameters such as ecology, genetics, evolution, physiology and development. That way, the different stages describing the individuals are inserted one after another following the individual life history. The life cycle also describes the transition between each class/stage, i.e. the vital rates, that is the probability of individuals going from a class to another. In the context of population modelling, life cycles allow the translation from individuals to population and the description of several events happening during the life of each individual, impacting the demography. Such events are birth, death, maturation, reproduction, growth, and their rates are influenced by given environmental factors and the individuals' ability to cope with these factors. In turn, one can model the population dynamics regarding the distributions of the stage spans and the survival rates (Alberts et al., 2003; Caswell, 2001; Manly, 1990; Townsend et al., 2003).

II.8 Life tables

Life tables describe the demographic parameters of a population, that is, the life-history traits in a very clear manner. These tables include:

(i) Groups gathering individuals by age classes and/or sexes or stages,

(ii) Number of individuals in each group/class,

(iii) Demographic parameters for each class such as mortality rates, mean lifetime, sex ratio etc.

Life tables are a translation of the life cycle in numbers since they indicate the proportion of individuals in each class over time and allow the estimation of the vital rates. Life tables are particularly useful for

managing population growth, as in the case of overcrowded situations (Bronikowski et al., 2016; Caswell, 2001; Etikan et al., 2017; Townsend et al., 2003).

II.9 Sex ratio

By definition, the sex ratio is a proportion between the number of males and females within a population presenting sexual reproduction. If the sex ratio is female-biased or/and the age structure is composed of numerous reproductive individuals, the birth rate can increase significantly (Hardy, 2002).

In human-modified landscapes, these population biology-related concepts remain of primary importance because animals respond or adapt to novel environments. Such adaptations include modifications of parameters such as mortality, birth rates and some life-history traits (through phenotypic plasticity for example (Kalbitzer et al., 2018)), which in turn impact population size, demography and dynamics, and depend on the carrying capacity of the environment. As a result, species populations can decline or thrive. The next section focuses on a specific case of a species evolutionary success under the human-primate interface. A common example of a successful adaptation to human-induced overlapping habitats is the long-tailed macaque, a species that flourishes impressively in environments shared with humans (Cords, 2012).

III Study case: the long-tailed macaque in Ubud, Bali

Within the Cercopithecidae family, the genus *Macaca* comprises 23 species, including *Macaca fascicularis* (Raffles, 1821), the long-tailed macaque, also named crab-eating macaque (Cords, 2012). Having cohabited with humans for millennia, macaques are especially concerned by the phenomenon of anthropogenic interface (Eudey, 2008; Fuentes, 2006; Lee, 2010; Mallapur, 2013; Schilaci et al., 2010). The long-tailed macaque, in particular, is a commensal primate, which means that its ecology is highly anthropogenic since it is frequently observed living in close association with humans (Brotcorne, Fuentes, et al., 2015).

As many tropical lands, Bali Island (Indonesia) has faced a high rate of deforestation following rapid agriculture expansion over the past centuries (Boquet, 2017), forcing many populations of macaques to cohabit with humans. Also, Hinduism culture is predominant in Bali, and many Hindu temple sites (and their surrounding forests) are prominent infrastructures scattered across the island. Many of these sanctuaries put *M. fascicularis* populations up, where the animal is sacred due to its position in Hinduism beliefs. Thus, Bali can be seen as a big "agricultural-religious system", where the human-primate interface is constantly present (Fuentes and Gamerl, 2005; Lane et al., 2010; Lane-deGraaf et al., 2014).

III.1 The increase of macaque population size in Ubud

In Bali, 43 populations of long-tailed macaques have been inventoried. The largest ones are those living at tourist sites (Lane et al., 2010), that is Hindu temple systems comprising each up to hundreds of monkeys. The Monkey Forest Sanctuary in Ubud shelters a population that has faced an incredible rise over the last decades, as we can see in Figure 2. And the population is now facing the highest density it has ever encountered, with 66 individuals per hectare (Brotcorne, 2014, 2019; Brotcorne, Maslarov, et al., 2014).

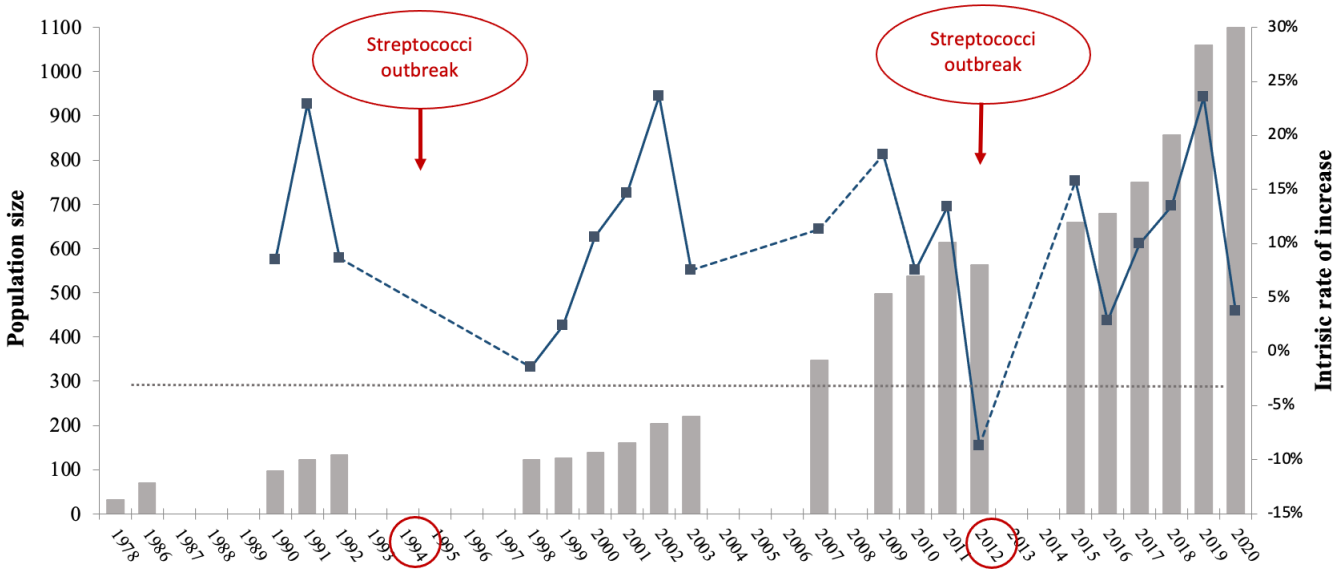


Figure 2: Long-tailed macaque population growth in Ubud, the past 40 years. The left vertical axis is the number of individuals (gray bar plot) and the intrinsic rate of increase is on the right vertical axis (blue lines). The presence of blue dotted lines is when counts are missing for one or several years. The two disease outbreaks faced in 1994 and 2012 are highlighted in red (Modified from Brotcorne, Fuentes, et al. (2015). University of Liège).

III.2 A highly flexible species and the causes of the demographic explosion in Ubud

A particularity of the genus *Macaca* is the broad distribution of the different species in a large range of habitats, resulting in an exceptional evolutionary success among primate groups (Cords, 2012; Eudey, 2008; Priston et al., 2013). The long-tailed macaque has, along with humans, rhesus macaque and baboon, the largest geographical distribution among primates (Fuentes, 2010; Lane et al., 2010; Priston et al., 2013). Indeed, the long-tailed macaque distribution spans across Southeast Asia (Figure 3), including some islands of the Indonesian Archipelago (Fuentes, 2010; IUCN, 2008; Lane et al., 2010; Pal et al., 2018).

Due to their wide distribution, the habitat of this monkey covers several biotopes, varying from mangrove and fens to primary and secondary growth forests (Eudey, 2008; Fuentes, 2010; IUCN, 2008). More specifically on the island of Bali, crab-eating macaques inhabit areas of diverse ecological conditions, e.g. on the coasts or beaches and in the scrubs, as well as in seasonal rainforests and of course, they share spatial and ecological overlap with humans in cities and the countryside. Thus, long-tailed macaques possess an ecological and behavioural flexibility and can adapt favourably to novel conditions, invading and proliferating easily in human-induced environments (Fuentes, 2010; Lane et al., 2010). They actually are synanthrope, that is "*an undomesticated animal that lives in close association with people and benefits from their surroundings and activities*" (Merriam-Webster, n.d.).



Figure 3: Geographical distribution of Macaca fascicularis. The species is widely distributed across Southeast Asia and particularly in Indonesia (IUCN, 2014 - Version 2019-1).

Combined with their eco-behavioural plasticity, these monkeys have a high diet flexibility: they are generalists and opportunists, which participates to their strong evolutionary success in human-altered environments. Indeed, they are omnivore (although mainly frugivorous) and possess a simple gut similar to the human one, providing them with the ability to digest quickly and adapt their diet incredibly fast (Lane et al., 2010; Luncz et al., 2017).

What are the factors responsible for this impressive population growth in Ubud? Macaques usually live in commensalism with humans, where they take advantage of suitable conditions. At Ubud Monkey Forest, macaques are highly provisioned due to touristic and cultural/religious reasons. Hence, the species takes advantage of human food resources in its nutritional requirements, due to its flexibility. Firstly, excess of food supplies consequently improves the reproductive abilities of females and ultimately, the birth rate rises (Asquith, 1989; van Noordwijk and van Schaik, 1987). Secondly, the vicinity to humans allows for

lower ecological pressure conditions. Indeed, in sanctuaries, macaques benefit from protection, refugia conditions with the absence of predator pressure and with ecological corridors, fitting perfectly well with the macaques' patterns of habitat use, foraging and dispersal. Therefore, the mortality rate decreases. These specific demographic conditions have led to a large population growth, and ultimately to a situation of overpopulation (Brotcorne, 2014; Brotcorne, Maslarov, et al., 2014; Fuentes, 2010; Fuentes and Gamerl, 2005; Fuentes, Shaw, et al., 2007; Lane et al., 2010; Peterson et al., 2013; Schilaci et al., 2010; Sih, Ferrari, et al., 2011). Further reinforced by a compression effect (along with natural habitat loss, many animals congregate in a specific beneficial habitat where resources are available), this turns into an overcrowding situation where an important density of animals regroups in a limited availability of space. Macaques in the wild live in groups and use different places in their home range for sleeping or eating, the groups migrate, and animals need space. In nature, food resources are seasonal, they fluctuate, and can become limited. Notice that a lack of resources can be total (e.g. a fire burns all the available food) or can be relative: the competition is too high and resources decrease (Townsend et al., 2003). In the specific case of Ubud, whereas food is abundant due to human supplies, the limited resource is space. Indeed, macaques are constricted in a 16 ha-forest patch which does not grow, contrary to population size. In turn, animals lack space and spread outside the forest, generating conflicts with human neighbours (Brotcorne, 2014; Brotcorne, Maslarov, et al., 2014; Cloutier et al., 2018; Fuentes, 2010; Fuentes and Gamerl, 2005; Fuentes, Shaw, et al., 2007; Lane et al., 2010; Peterson et al., 2013; Schilaci et al., 2010; Sih, Ferrari, et al., 2011).

III.3 Study species socio-ecology and the consequences of overcrowding

Overcrowding has social and physiological consequences because competition for space and resources becomes more present, the social tension amongst macaques increases and living conditions deteriorate. Moreover, it ultimately leads to major inter-specific conflicts, endangering macaques and people.

Lately, following overpopulation and lack of space, monkeys spread around the Monkey Forest. Their invasion into the surrounding villages (Ubud and Padangtegal) increased substantially along with the conflict for space and food (Schilaci et al., 2010), leading to crop raiding and infrastructure damaging, vendor shop-stall robbing, house invading and stealing and in turn, to anger and fear from the locals towards the animals perceived as pests (Fuentes, 2013; Lee and Priston, 2005; Peterson et al., 2013; Priston et al., 2013). At tourist sites, people and monkey interactions can result in aggressions, sometimes with severe injuries (Fuentes and Gamerl, 2005; Lane et al., 2010; Mallapur, 2013; Priston et al., 2013). Also, contact between primates and humans enhances the risk of disease transfer in both directions (Fuentes, 2010). For example, two *Streptococcus* disease outbreaks (Figure 2) affecting macaques already happened in the Ubud population history, probably due to a zoonotic case of transmission from domestic animals to macaques (Brotcorne, Fuentes, et al., 2015).

Finally, most primates, including *Homo sapiens*, live in social groups, where a complex structure and an organisation are clearly defined. The social organisation typically is "who lives with whom" and is defined by several parameters such as the sex ratio, the group fission and fusion dynamics and the diversity among the populations/species (Cords, 2012; Schülke et al., 2012). *M. fascicularis* shows a multimale-multifemale structure and a female philopatry in which females remain in their natal group for their whole life while males disperse across groups after puberty (4 years old) (Lane et al., 2010; van Noordwijk and van Schaik, 1987). Males are likely to live in different groups during their life, which drives the gene flow and produces a highly dynamic demographic structure. They show inter-group dispersal, most of the time approaching and interacting with sexually receptive females during the migration process (Cords, 2012; Pal et al., 2018; Sueur et al., 2008).

Usually, a population of long-tailed macaques includes several matrifocal groups of different size but the total group can reach up to 200 individuals (Lane et al., 2010), as observed in Ubud population (Brotcorne, 2014). In such an organisation, the stable core of the group rests upon matrilines (i.e. "*derivation of lineage through the mother instead of the father; social group revolving around female kinship*") (Wisconsin-National-Primate-Research-Center, 2011), around which the rest of the group self-organises. Matrilines "*set the stage for extensive cooperative bonding among female kin, which stay together for life*" (Cords, 2012). Therefore, in the long-tailed macaque's social organisation, the adult sex ratio is biased towards females, and social groups are female-bonded (Cords, 2012; Schülke et al., 2012; van Noordwijk and van Schaik, 1987). *M. fascicularis* presents a social structure based on inter-female relationships where there are matrilineal hierarchies. Mothers have a higher rank than daughters and sisters rank is inversely linked to their age. Usually, daughters inherit from their mother rank and every kin from a matriline outranks all members of another matriline (Cords, 2012; de Ruiter et al., 1998; Holekamp et al., 1991; Lane et al., 2010; Schülke et al., 2012; Seyfarth et al., 2012).

While many different patterns exist among primates, *M. fascicularis* exhibits a polygamous and promiscuous mating system, that is both females and males mate with several mating partners (Nikitopoulos et al., 2005; Schülke et al., 2012). Long-tailed macaques reproduce and give birth throughout the year. But peaks of births are usually observed, depending on the geographical range (Kavanagh et al., 1984; Pal et al., 2018). Sexual maturity is reached at around 6 years for males and 3.5 for females (Fooden, 1995; Saltzman et al., 2011).

In the Ubud Monkey Forest, animals get used to humans, approach them with less fear and become more terrestrial in order to collect supplementary food from provisioning. These living conditions have several influences on the macaque individuals (behaviour, activity), groups (structure, organisation), and population (dynamics) (Brotcorne, 2014). First, studies showed that male emigration decreases severely, which can influence genetic diversity (Lane et al., 2010) and have dramatic impacts on social structure and reproduction. Second, macaques habituate to tourist schedules to facilitate their supplemental food acquisition by changing their activity patterns (Giraud, 2015; Lane et al., 2010; Mallapur, 2013; Sha et al., 2013). Furthermore, overcrowding affects social interactions significantly. Ultimately macaque well-being and long-term survival as well as the population wellness might be threatened. Finally, as social group size increases together

with population size, a common phenomenon is the fission of social groups when the density becomes too important. Such events have happened several times over the past years in the Ubud population and have modified the population structure and the social organisation (Brotcorne, 2014; Cloutier et al., 2018; Giraud, 2015; van Schaik et al., 1986).

In population management, it is primordial to consider the factors influencing the parameters upon which the population trends rest. In this context, we are particularly interested in the values of the survival rates and the fecundity of the individuals. Several elements (population density, provisioning, behaviour, social structure) can affect such parameters, and the impact can vary directly or indirectly between classes. But in the context of the Ubud Monkey Forest population control, we will only focus on the factors influencing the female reproductive success, expressed here as birth rates (fecundity), offspring survival and female survival, regarding the central role of females in the birth control program (see below).

In most primates, competition between females stems from the offspring quality and number (Fedigan, 1983). Obviously, natural selection should favour any female trait driving a better offspring genetic aspect in the following generation. Thus, females compete via the established (intra- and inter-group) hierarchy, where higher ranked individuals will benefit from a better quality of food and easier access to it, as well as from a safer spatial position in the social group (Harcourt, 1987; Isbell, 1991; Sapolsky, 2005; van Noordwijk and van Schaik, 1988). The major consequence is the difference in health status between the dominant and subordinate females. Indeed, feeding properly and sufficiently enhances health, and a more central position within the social group allows for less predation and risks of disease. Furthermore, males are usually more interested in high-ranking females (van Noordwijk and van Schaik, 1985), which bring them closer to the females and in turn guarantees protection and social interactions for the females (Girard-Buttoz et al., 2014; van Noordwijk, 1985; van Noordwijk and van Schaik, 1985, 1987). Lower ranked females are sometimes lacking nutritional resources and become more peripheral. They get less social interactions, are forced to invest more energy in foraging and are more exposed to predation (Isbell, 1991; van Noordwijk and van Schaik, 1987, 1988). They also often suffer from intimidation and harassment from dominant females (Brotcorne, 2014; van Noordwijk and van Schaik, 1987). All in all, lower ranked females are more subjected to social and nutritional stress likely to reduce their quality of life and ecological fitness.

It is therefore biologically significant to assume that hierarchical position influences the female reproductive success. First, better nutrition, safety and social interactions (i.e. less stress) provide a higher chance to survive. This is particularly the case in free-ranging provisioned populations where food is clumped, offering further opportunities to higher-ranked individuals to monopolise the food (Whitten, 1983). Moreover, better the quality and quantity of food a female can get, higher the birth rate and survival of young infants will be (van Noordwijk and van Schaik, 1999; Whitten, 1983). Proximity with males may also ensure higher frequency of copulation and so higher chance of being fertilised, ultimately increasing birth rate. Furthermore, social stress conditions affect low-ranking females through disruption of their reproductive cycles, resulting in lowered fecundity (van Noordwijk and van Schaik, 1985, 1987). In this case, offspring survival mainly relies on maternal condition, care and predation. In the Ubud population, predation is rare so it can be neglected (Brotcorne, 2014). However, females with a higher hierarchical position benefit more from

allo-caring from other females and kin, which enhances survival of their offspring (Onishi et al., 2011). Consequently, high-ranking females are supposed to have higher fertility, survival and offspring survival, although the subject is still controversial (Fedigan, 1983; Harcourt, 1987; van Noordwijk and van Schaik, 1999). Actually, many studies suggest that fertility, offspring survival and female survival are positively correlated with rank. Yet while some lead to statistically significant results (Borries et al., 1991; Drickamer, 1974; Pusey et al., 1997; van Noordwijk and van Schaik, 1999; Wasser et al., 2004), others did not (Berman, 1988; Gouzoules et al., 1982; Paul et al., 1990; Takahata et al., 1999; van Noordwijk and van Schaik, 1999; Wolfe, 1984). Most of the time, significant results occurred when rank effect was combined with other effects such as density and resource availability (e.g. provisioning versus food scarcity) (van Noordwijk and van Schaik, 1999).

The number of infants and their survival is important in population dynamics as they indicate a good population turnover (Townsend et al., 2003). Offspring survival, as cited above, is directly linked to the mother's condition, which also includes the maternal behaviour. Offspring mortality rate should thus be higher for nulliparous females than parous ones, mainly due to malnutrition and mishandling of the infant (Fedigan et al., 1986; Koyama et al., 1992; Naiken et al., 2015; Smuts et al., 1989; Sunderland et al., 2008; Tsuchida et al., 2008).

III.4 Management solutions regarding the overcrowding situation

Considering the current conflicts between macaques and people, as well as the increased social tension amongst the macaques, both arising from the overcrowded situation, the Ubud population wellbeing and the long-term coexistence with humans are jeopardized and require to develop management plans. Taking an "ethnoprimatological" perspective (i.e. "*anthropogenic elements such as social, economic and cultural must be included in the inquiry of primatology*" (Fuentes, 2010)) is necessary in this shared environment, where every solution must involve a multidisciplinary approach to be appropriate and efficient.

An obvious solution is the reduction of provisioning, to make food a limited resource and lower the carrying capacity (K) of the environment (see above), in order to provoke a self-regulation of the population via density factors. In fact, when food availability decreases, fecundity and survival are supposed to decrease because competition for resources increases. In turn, the population size should reduce itself (Townsend et al., 2003). But, managing food resources is actually hard to achieve. First, due to overpopulation driven by lack of space, macaques expand beyond their forest range to avoid competition and to feed on alternative food, making feeding control difficult. Secondly, preventing provisioning at the temple touristic site goes against the Hindu traditions, as monkeys receive offerings because of their sacred position (Fuentes, 2010; Fuentes and Gamerl, 2005; Mallapur, 2013; Radhakrishna, 2013; Schilaci et al., 2010). Finally, provisioning represents a strategy for managers to maintain the macaques inside the sanctuary, thereby reducing the nuisances they cause to surrounded properties and crops. For example, during the recent Covid-related lockdown, when food supplies by tourists drastically decreased, monkeys ranged outside the sanctuary more intensively, which increased the conflicts with people living in the surroundings (Brotcorne, personal

comm.).

Other solutions for population control should therefore be taken into consideration. Lethal strategy consists in culling animals to augment the mortality rate and diminish the population size. Another method is translocation or relocation where selected individuals of the population are moved to another place. These two methods have the same purpose as they quickly decrease the number of individuals in the population (Townsend et al., 2003). However, they are not suitable for several reasons. Firstly, we cannot neither kill nor move macaques because of their key roles in Hinduist culture and economic importance in this place. Moreover, translocation/relocation imposes a significant financial cost (Lee, 2010) and often remains inappropriate due to the lack of alternative suitable habitat and/or inter- or intraspecific conflicts at the new site (Lee and Priston, 2005). Finally, theory of density-dependent logistic growth tells us that if population size is reduced but not the habitat carrying capacity K, competition for resources will decrease and the population will continue growing and soon reach the previous population size (Caswell, 2001; OpenStax, 2020). These methods thus provide a short-term solution, only postponing the high-density population problem. An alternative method consists of controlling the birth rates, by sterilising individuals. It is sustainable, less costly, more ethical and in better adequacy with the local culture (Brotcorne, 2014; Lee and Priston, 2005). In these conditions, sterilised individuals still use resources and thus, the problem of density-dependant growth does not occur.

IV The birth control program and the matrix population model

The managers and scientific collaborators of the Ubud Monkey Forest (University of Liège and Universitas Udayana) have chosen the last option to control the population growth at this site. Three years ago, they started a sterilisation program based on tubectomy (i.e. ligature of fallopian tubes) of reproductive females, given the key role of females in the social structure and organisation. The main demographic objective of this program is to reach a null population growth, leading to population size stabilisation. To properly plan the birth control program, some PVA have been assessed, including a matrix population model established in 2017. It is based on demographic long-term life tables dating back 11 years ago. This model helped to estimate the number of females to sterilise in order to diminish the fecundity on the population dynamics, and in turn, to reach the null population growth (Brotcorne, 2019; Cloutier et al., 2018). The model is constructed as follows.

IV.1 Biological stages

The model is stage-structured, meaning that it is based on significant biological stages in the species life cycle (Caswell, 2001). Here, the stages are defined according to age and sex of the macaques (Cloutier et al., 2018). The different stages are represented in Table 1 and refer to the age/sex class identification represented on Figure 4. Note that three out of the stages are only age-structured, because the sex of the individuals is impossible to determine in the field before the macaque reaches about 3 years old (Brotcorne, 2014; Cloutier et al., 2018).

Stages	Class	Corresponding picture on figure 4	Sex	Age interval (years)
Stage 1	Infant	1-2	Genderless	0-1
Stage 2	Juvenile 1	3	Genderless	1-2
Stage 3	Juvenile 2	4	Genderless	2-3
Stage 4	Subadult	5	Female	3-4
Stage 5	Adult	6	Female	>4
Stage 6	Juvenile'	4	Male	3-4
Stage 7	Subadult	7	Male	4-5
Stage 8	Subadult'	7	Male	5-6
Stage 9	Adult	8	Male	>6

Table 1: Description of the age and sex stages of the life cycle used to construct the matrix population model. Modified from Cloutier et al. (2018).



Figure 4: Pictures illustrating each age/sex stage used in the field for the census and observations and represented in the matrix population model in 2017 (Cloutier et al., 2018).

IV.2 Life cycle graph

Typically in stage-based models, we build a life cycle which creates a relation between individuals and the population (Caswell, 2001). Figure 5 shows the life cycle graph of the matrix population model developed three years ago by Fanny Cloutier and Pr. Nicolas Schtickzelle, where the different parameters of the population are represented. The stages (referring to Table 1) are the circled numbers and each arrow represents a transition from one stage to the next. These transitions summarise the probabilities (P) of all possible events that can happen from one stage to the next. Here, transitions concern only the survival rates (S) and fecundity rates (F) (expressed as birth rates) (Cloutier et al., 2018).

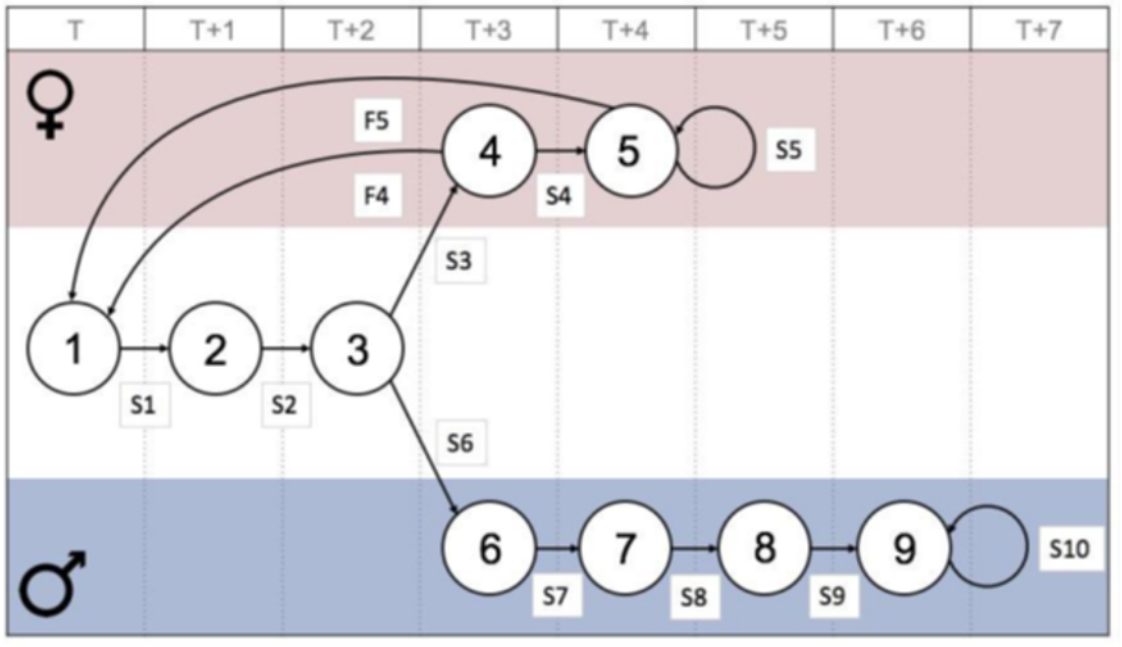


Figure 5: Life cycle of the matrix population model developed for the macaque population of Ubud in 2017. Legend: The stages are represented by circles. The arrows between the stages are the survival rates (S) and the fecundity (F), which represent births (Cloutier et al., 2018).

IV.3 Matrix population model functioning and geometric growth rate

In such models, instead of considering the time as a continuous variable, the model is constructed over discrete time steps (Alberts et al., 2003; Caswell, 2001). Here, the step time is of 1 year and refers to the transition from one age-stage to the next one (Cloutier et al., 2018). Thus, modelling a life cycle into discrete time (t) is done by several equations which describe the transition from time t to time $t+1$. For instance, the number (N) of infants at time $t+1$ depends on the following equation:

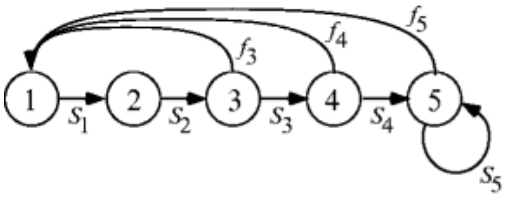
$$N_1(t+1) = N_4(t) \times F4 + N_5(t) \times F5 \tag{1}$$

Where N_4 and N_5 are respectively the number of subadult and adult females the year before and F the

respective birth rates. The number of individuals at each stage will therefore be respectively represented by an equation constructed as Equation 1, building ultimately a set of equations. This set can afterwards be converted into a matrix form, called the Leslie matrix where the different parameters (F and S) are the matrix coefficients. The model is thus based on matrix calculus as in Figure 6, where the Leslie matrix allows evaluating how the composition of the population varies from one time step to the next one and projecting the population over a period of time (Alberts et al., 2003; Caswell, 2001). Figure 7 is a complete example illustrating the functioning of a matrix population model for a population structured in five stages (Charles et al., 2009).

$$\begin{bmatrix} n_0 \\ n_1 \\ \vdots \\ n_{\omega-1} \end{bmatrix}_{t+1} = \begin{bmatrix} f_0 & f_1 & f_2 & \dots & f_{\omega-2} & f_{\omega-1} \\ s_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_2 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & s_{\omega-2} & 0 \end{bmatrix} \begin{bmatrix} n_0 \\ n_1 \\ \vdots \\ n_{\omega-1} \end{bmatrix}_t$$

Figure 6: Matrix population models basic functioning. The number of individuals at each stage for time $t+1$ is represented by the left vector, the Lefkovitch matrix with the respective equations coefficients is in the centre and the numbers of individuals at time t are into the right vector. ω is the last stage the individuals can reach (Caswell, 2001).



$$\mathbf{A} = \begin{pmatrix} 0 & 0 & f_3 & f_4 & f_5 \\ s_1 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 \\ 0 & 0 & 0 & s_4 & s_5 \end{pmatrix}$$

$$\begin{cases} n_1(t+1) = f_3 n_3(t) + f_4 n_4(t) + f_5 n_5(t) \\ n_2(t+1) = s_1 n_1(t) \\ n_3(t+1) = s_2 n_2(t) \\ n_4(t+1) = s_3 n_3(t) \\ n_5(t+1) = s_4 n_4(t) + s_5 n_5(t) \end{cases} \Leftrightarrow N(t+1) = \mathbf{A}N(t)$$

Figure 7: Example of a matrix population model of a population structured in 5 stages. On the left upper figure: the representation in a life cycle graph with the stages in circles and the arrows of the transition probabilities (F and S); the right upper matrix is the Leslie matrix; on the left down corner are the different equations for each stage and on the right down corner the generalised equation for the model (Charles et al., 2009).

Eventually, the model allows the calculation of the growth rate. The growth rate of the population over discrete time steps is called the geometric growth rate (λ). It describes abundance (N_{t+1}) next year as a proportion of the abundance this year (N_t). When λ = 1, a population remains constant in size over time. The main approach is developed from this equation (Caswell, 2001):

$$N_{t+1} = N_t \times \lambda \tag{2}$$

IV.4 The birth control program linked to the populatio biology

The main demographic objective of the birth control program in Ubud Monkey Forest is to hold the population growth rate back by reaching a null growth. That is, establishing $\lambda = 1$ and maintaining a plateau of the population growth. Thus, it is necessary to follow the progress of the population growth and birth rates. Three years ago, Fanny Cloutier and Pr. Nicolas Schtickzelle evaluated that 52% of adult females should be sterilised to reach a temporary null-growth. The last campaign to reach the proportion of 52%, that is, 140 females (Brotcorne, 2019), took place in August 2019. The objective was almost reached since 137 females were sterilised in total (over a two-year period of time) and 6 of them have died since then. The model established in 2017 was deterministic and computed a sterilisation rate that could reduce the overcrowded population growth rate (λ) to 1. However, because this model does not consider the reality of the current population such as the actual proportions of sterile females and important behavioural characteristics, it must be improved. Hierarchical rank and maternal experience are expected to influence female and offspring survival and fecundity. They are hence pertinent parameters to test statistically and to consider into the improved model.

V Study objectives

As a part of the population management project, the scope of this thesis is to refine the matrix model of the high-density population that has been subjected to birth control for three years. The goal is to assess the demographic outcomes of the current sterilisation program by (1) enhancing the model with the inclusion of the updated demographic data, which will allow to (2) incorporate new stages and parameters by considering the updated demographic data, as well as ethological data such as the hierarchical status and the maternal experience of the females; (3) running projections to set new predictions on the population trend.

V.1 Include the updated demographic data

The initial model was based on counting data collected from 2009 to 2017. I will therefore update the novel model by including more recent census data, collected in 2018, 2019 and 2020.

V.2 Refine the predictions by introducing new stages and parameters to the model

I will improve the current deterministic model to drive it more realistic with other stages and parameters. By doing so, I should be able to refine the predictions on the population trends and dynamics. Such parameters include:

a) *The sterilised females:*

The first objective will allow in the meantime, to include the proportion of females already sterilised into the model. I will also consider the number of pregnant females that were captured for sterilisation during the sterilisation campaigns and the mortality of the sterilised females.

b) *The hierarchical status of the females:*

Firstly, I will define the hierarchical ranking status of the females based on The Social Network Analysis data available for one specific group ("Michelin") of the population. Then the relation between the female respective reproductive success such as fecundity, female survival and offspring survival, and their hierarchical ranking status will be tested. Finally, I will introduce the ranking status into the model. The previous model considered all females with the same fertility and survival rates and did not take into account differences in offspring survivals. By including the ranking status of the females, I would be able to discriminate fecundity, as well as female and offspring survival variations into the model. By establishing the potential impact of the female ranking status in the social group, I could:

- Be able to better understand if their rank could impact their fertility rate, female survival rate and offspring survival rate,

- Assess if these rate variations could impact the demographic trends of the population, and thus, the sterilisation rate.

c) *The maternal experience of the females:*

With the data collected from the Michelin group, I will establish approximate survival rates for the infants born from nullipara females (i.e. subadult females). Following the higher risks of infant loss specific to subadults, survival rate should be lower for nullipara females than the one for the infants having a primi- or multipare mother (adult females). The previous model did not consider the differences in infant survival rates. By including this parameter, I could:

- Be able to better understand if the maternal experience of a female could impact the survival rates of the infants,
- Assess if these rate variations could impact the demographic trends of the population, and thus, the sterilisation rate.

Since data about the hierarchical ranking status and the follow-up of the females are the most complete in the Michelin group, the data analyses of female fecundities, survival and offspring survival will be based on the data (censuses and histories) from this group only. Then, I will infer the results at the population scale for the construction of the new matrix population model.

V.3 Projections and stochasticity

Some unpredictable events such as disease outbreaks can significantly influence the vital rates of the population. The population under birth control could potentially be subjected to such a crisis and should be able to survive and stabilise on the long-term. Thus, including a temporal variability in the model, by taking into account such events, could provide a higher level of safety.

By integrating stochasticity, instead of obtaining a fixed number of individuals to sterilise, I should be able to get a confidence interval around the sterilisation rate. The introduction of this interval in the model will allow to establish a more progressive sterilisation rate and to diminish the risk of exceeding the maximum sterilisation threshold. Indeed, since the sterilisation campaigns spread out over several years, the introduction of new fertile females into the population causes the latter to stabilise more slowly. Therefore, putting stochastic parameters into the model should enable me to review the percentage of sterilised females per year, and the impacts of these sterilisation proportions on the demography and dynamics of the population.

With these data, I will be able to re-estimate the demographic parameters of the model (S and F), to establish new predictions and eventually to assess the demographic outcomes of the current sterilisation program. Thereby, I could improve the estimation of the sterilisation rate necessary to reach the stabilisation of the population growth.

SYNTHESIS OF COLLECTED DATA

I Material and method

I.1 Study site

Bali is a small island of 5600 km^2 highly populated with 4 millions of inhabitants (Boquet, 2017). The Ubud Monkey Forest Sanctuary is situated next to the villages of Padangtegal and Ubud and shelters a large long-tailed macaque population. This site contains 16 ha of mixed forest, three temples and several shrines and statues. Around the Monkey Forest, rice fields, roads and rivers are present. Because of the monkeys' proximity and its natural-cultural beauty, the site is visited by more than 100,000 tourists every year (Fuentes and Gamerl, 2005).

I.2 Study population

The first reports of the Ubud Monkey Forest population date back to 1968, when the local villagers counted 23 macaques (Wheatley et al., 1994). Since then, several studies took place for assessing the progression of the population demography and dynamics over time. Even though the population faced two disease outbreaks, in 1994 and in 2012, it has shown a dramatic growth since the 70's. Indeed, as we can see on the chart represented on Figure 2, the population grew from 69 individuals in 1989 to 1011 in February 2020. In 2019, the population counted 1103 individuals split into seven social groups, called Michelin, Central, Cemetery, East, Temple, Selatan and New Forest respectively. The Michelin group split into two groups, called Michelin and Utara, recently in 2020.

I.3 Demographic data

To model the population trends and construct my matrix population model, I used censuses collected yearly between 2009 and 2020. The census method consists in counting directly the individuals in each social group based on the age and sex classes defined previously by F. Cloutier and F. Brotcorne (Figure 4 and Table 1) (Cloutier et al., 2018). The objective of direct head counting each year and for many years is to

give consistent demographic data for each group and thus the whole population, upon which I can base my model. From the updated data set I calculated the logistic growth rate (λ) from 2009 to 2020, with Equation 2 described previously (Section IV.3).

Since the sterilisation campaigns began in 2017, it was necessary to include some modifications directly into the censuses between 2017 and 2020, in order to consider the new sterilised subadult and adult females, the mortality of the females (sometimes due to surgery and sometimes to other factors) and the proportions of pregnant females that were sterilised during the campaigns.

I.4 Ethological data

My work consisted among others in considering and including new and more complex parameters such as the effect of female rank and maternal experience on their reproductive success, expressed as fecundity, female survival and offspring survival.

a) *Effect of female hierarchical rank on their reproductive success*

In the field, I collected behaviour data based on two months of observations of the Michelin group, to establish the females' hierarchy. The Michelin group served as a baseline for the parameters for the population model construction. Michelin is the best followed and well-known group in the Ubud Monkey Forest population, thanks to G. Giraud's PhD work about social network.

Fifteen minutes focal samples have been conducted, as well as proximity scans. This sampling method was carried out on 54 identified individuals from the Michelin group: 14 males and 40 females. Using a pre-established ethogram (Brotcorne, 2014) the individuals were followed, and their behaviour was recorded using the app « Animal Behaviour Pro » (available on Ipad®), with a special focus on the patterns of agonistic and affiliative behaviours. The proximity scans consisted of counting the number of neighbour individuals in a pre-determined radius (body contact, $< 1m$, $< 3m$ and $< 5m$) every 5 minutes around the focal subject (0, 5, 10 and 15 minutes). Counting was realised according to the age/sex classes (Table 1 and Figure 4) or the identity of neighbours when known. In order to obtain reliable and analysable results, my goal was to reach 45 minutes of focal observations for most of individuals, thus a threshold of 3 focal samples per individual (total number = 141 focal samples; that is, 35.25 hours in total). From these focal samples, I built the directional dominance matrices based on all agonistic interactions and their outcome (identity of the winner vs loser). Then, G. Giraud established the hierarchy between females using the David's Score (*DS*) method. *DS* estimates an individual's rank based on agonistic encounters by considering the ratio of successes within each dyad (Bang et al., 2010; Bayly et al., 2006; David, 1987; Gammell et al., 2003).

After the establishment of the females' hierarchy, I used a follow-up data set collected between 2017 and 2019 on the Michelin group to trace the history of the females present in the established hierarchy. These data allowed me to estimate the number of female-year observations (fy), which are the number of years a female was observed (National-Research-Council, 1981), as well as the yearly births per

female and the survival of their offspring from birth (infant stage) until 1 year old (juvenile 1 (J1) stage). The latter are the explanatory binary variables (success or failure) used in the further statistical analyses. The data set comprises 101 fy and 69 infants born over the years. Note that the follow-up data of the Michelin group had many missing values on the offspring histories, mainly due to time constraints of field missions. Therefore, I determined a threshold of 8 months from birth at which the offspring could be considered as a survivor J1, and so noted as "success".

Statistical analyses were run to test the following null hypotheses: fecundity and offspring survival do not depend on females rank status. To test whether fecundity and offspring survival depend on the female rank status, logistic regression models (α=0.05) were performed in R® software (version 4.0.2), with the rank as the explanatory variable and the birth and survival (success vs failure) of offspring as the response variables. The female identity was considered as a random variable, and sterile females were considered as missing data (NA) from the year of their sterilisation. After testing the effect of the rank as an ordinal variable, I also treated the rank as a categorical variable by dividing the number of females into two sub-groups: the first half of the females representing the "high-ranking" (or dominant) females and the other half the "low-ranking" (or subordinate) females. I ran the same analyses by considering these groups instead of the exact rank per female. I finally calculated the mean birth rates of each sub-group, based on the following equation:

$$\bar{BR} = I_t/2 \times fy \tag{3}$$

Where I_t = the total number of infants born in the group and fy is the total number of female-year observations (National-Research-Council, 1981). The survival rate of the infants (SR) was calculated as follows:

$$SR = J1/I \tag{4}$$

Where $J1$ = the number of females offspring that survived until at least 8 months after birth, and I = the number of infants (National-Research-Council, 1981). Not enough data about the effect of the rank of the females on their own survival was available in the data sets to run proper analyses.

In turn, the results on female rank effect on reproduction will be added to the matrix population model as a covariate likely to impact the birth rates in females and survival of offspring.

b) *Effect of female maternal experience on the offspring survival*

To study the differences in offspring survival between the nulliparous (subadults or SF) and primi- or multiparous females (adults or AF), I used the same follow-up data set as for the rank analyses previously cited. However, I traced the history between 2017 and 2019 of all known females from Michelin group instead of only the ones studied for the hierarchy. After tracing the history of females from the Michelin group, I calculated the number of subadult females and adult females each year and estimated the birth rates and offspring survival rates in each group. Birth rates were estimated based on the following definition: total number of infants per total SF or AF (Equation 3). The survival

rate of the infants (SR) was calculated as Equation 4. Only descriptive analyses were conducted with these results.

II Results

II.1 Demographic data

The new data set that was used for the model construction is shown in Table 2. As we can see in the table, I added two new stages compared to the censuses used in F. Cloutier's thesis: sterilised subadult females (nobs4s) and sterilised adult females (nobs5s). I also directly included factors related to the sterilisation campaigns into the censuses:

- A subadult female captured and successfully sterilised at year $= t$ was considered as a sterilised subadult female that year, but as a sterilised adult female at year $= t + 1$.
- Similarly, a pregnant female captured and sterilised at year $= t$ was considered as fertile for this year and sterile only from the year following the surgery ($t + 1$). In fact, since tubectomy does not interfere with the gestation process (Deleuze et al., in prep.), the female could give birth the year of her surgery and would no longer give birth the years after surgery.
- Some causalities (death or disappearance, 6 in total) happened during or shortly after every campaign. These were considered into the census data by removing the number of deaths directly from the annual counts at the right stage.

	nobs1	**nobs2**	**nobs36**	**nobs4**	**nobs4s**	**nobs5**	**nobs5s**	**nobs78**	**nobs9**	**TOTAL**	λ
	0-1 yr	**1-2 yr**	**2-4 yr**	**3-4 yr**	**3-4 yr**	**> 4 yr**	**> 4 yr**	**4-6 yr**	**> 6 yr**		
	INFANTS	**J1**	**J2**	**SF**	**SF steril**	**AF**	**AF steril**	**SM**	**AM**		
2009	83	68	92	27	0	155	0	39	34	498	/
2010	92	76	97	31	0	177	0	30	35	538	1.08
2011	90	91	118	37	0	197	0	39	44	616	1.14
2012	98	60	107	34	0	166	0	52	46	563	0.91
2014	100	86	108	32	0	218	0	50	65	659	1.17
2016	119	98	92	30	0	248	0	33	58	678	1.03
2017	119	118	167	29	0	201	16	34	63	747	1.10
2018	130	147	182	24	0	209	36	46	82	856	1.15
2019	169	189	203	19	12	211	90	82	82	1057	1.23
2020	182	126	187	40	0	234	131	82	117	1099	1.04

Table 2: Results of census data from 2009 to 2020 for each age-sex class and for the total population, with the corresponding values of the annual growth rates. Names of the age and sex stages/classes from left to right: J1 = juveniles 1, J2 = juveniles 2, SF = subadult females, SF sterile = subadult females sterilised, AF = adult females, AF sterile = Adult females sterilised, SM = subadult males, AM = adult males.

For example, in 2017 22 females were sterilised, including 4 pregnant females and 2 post-op deaths. The total number of sterile adult females for 2017 is therefore 16, since 2 females died and were removed from the census and 4 were pregnant. These 4 females were counted as sterile adult females only from year 2018.

Table 2 also shows the annual logistic growth rate. As we can see, the population size is increasing with a mean growth of 10% per year ($\bar{\lambda}$ = 1.1), except for the year 2012 when a *Streptococcus* outbreak occurred (Brotcorne, 2014). Nevertheless, the 2020 growth rate is lower compared to 2017, 2018 and 2019, which could be due to the proportion of sterilised females in the population even though no conclusion can be drawn for now, as we do not have enough step back.

II.2 Ethological data

a) *Effect of female hierarchical status on their reproductive success*

The results of the female rank status and the data of their respective birth and offspring survival are in Appendix A. These results were used for the logistic regression. Whether we consider the rank as the exact position in the hierarchy or as two groups (high- vs low-ranking), there was no significant effect of the rank on the birth rates nor the survival rates of the offspring. The means of birth and survival rates for the Michelin group are presented in Table 3. Given these means, we can tell that there is no clear difference in birth and offspring survival rates between the high- and low-ranking females. In conclusion one can say that there is no difference in fecundities and offspring survival according to the female rank status or, if there are differences in reality, these differences are too small to be statistically significant.

Category	fy	Infants	Survivors	BR	SR
Total	101	69	58	0.34	0.84
High-ranking	55	37	32	0.34	0.58
Low-ranking	46	32	26	0.35	0.57

Table 3: Empirical results of the influence of maternal rank status on birth rate and offspring survival rates from 0-1 year old, for data collected between 2017 and 2020. fy = female-years observations; $Infants$ = number of infants; $Survivors$ = number of offspring that survived from infant (0 year old) until at least 8 months old; BR = birth rate; SR = survival rate of offspring.

b) *Effect of female maternal experience on the offspring survival*

The results are in Appendix B. We lack enough data to test the question of the maternal experience effect. Indeed, the data set comprised enough subadult females only for year 2019 (9 SF) and only three of them had an infant, from which 2 survived until J1. While there were at least 22 adult females each year from which many infants were born. Regarding this poor data set, no robust comparisons between SF and AF could be made. The hypothesis assuming that the more a mother has maternal experience the more her infant can survive could not be tested and hence no conclusion could be drawn.

MODEL CONSTRUCTION

The construction of the new model was achieved in two main steps: first theoretically and second statistically. Each step included different reflections and methods of decision to obtain a simplified and accurate model (referred to as "final model") of the Ubud Monkey Forest macaque population. In turn, the final model was implemented into the statistical computer program SAS® (9.4 version), which estimated the required parameters allowing population projections and stochastic analyses.

In this kind of study, parameter selection and thus model simplifications are essential steps: only the solid and relevant parameters can be retained and introduced into the model in order to enhance the suitability of the model to the censuses. Indeed, the estimation of many parameters from a small data set can generate biases and large uncertainties into the model parameter estimates, which we want to prevent, to assure that the model is useful for reliable demographic projections. A summary of the different decisions and simplifications is in Table 4.

Stages or parameter	**Criteria**	**Theoretical simplifications**			**SAS® modeling**
		Complete model	First simplifications	Reasonable model	Final model
INFANTS	Sexes	yes	no	no	no
	Mother's maternal experience	yes	yes	no	no
	Mother's rank	yes	yes	yes	no
J1	Sexes	yes	no	no	no
	Mother's maternal experience	yes	yes	no	no
	Mother's rank	yes	yes	no	no
J2	Sexes	yes	no	no	no
	Rank	yes	no	no	no
SF	Reproductive abilities	yes	yes	yes	yes
	Rank	yes	yes	yes	no
	Sterile + rank	yes	no	no	no
AF	Reproductive abilities	yes	yes	yes	yes
	Rank	yes	yes	yes	no
	Sterile + rank	yes	no	no	no
J2'	Same as previous model	yes	yes	yes	yes
SM	Same as previous model	yes	yes	yes	yes
SM'	Same as previous model	yes	yes	yes	yes
AM	Same as previous model	yes	yes	yes	yes
C	Same as previous model	yes	yes	yes	no

Table 4: Summary of the different simplifications from the complete model to the final model (tested in SAS®). *C* = disease outbreak parameter; yes = stage or parameter kept into the model; no = stage or parameter discarded from the model.

I Theoretical creation and description of the model

In a first time, I relied on the age and sex classes which are represented in Table 1 and Figure 4, as well as on the life-cycle graph created by F. Cloutier (Figure 5) three years ago to imagine a new model describing the Ubud Monkey Forest macaque population dynamics. Different models were imagined during this step, throughout reflections and based on common sense to represent the population at best.

I.1 Complete model

I established a "Complete and theoretical model" illustrated in Figure 8 which answers the question: "In accordance with the population reality, what is relevant and/or biologically justified?" The complete model I elaborated from this question is the most exhaustive and representative of the population as it takes into account all the possible stages and parameters that can describe it. It is a complex, theoretical and very realistic model, biologically speaking.

First of all, all macaques should be distinguished between males and females from birth and through their lives, as they are born male or female and their respective survival over time depends on the sexes.

Secondly, offspring survival during the first year of life is supposed to vary according to the rank status and the maternal experience of the mother, as specified in the introduction. Stage 1 should be separated into different parallel stages where the survival rates vary according to the mother situation. For instance, survival of infants female would vary like: AF high-ranking ($1A_{AF}$) > AF low-ranking ($1B_{AF}$) > SF high-ranking ($1A_{SF}$) > SF low-ranking ($1B_{SF}$).

Furthermore, female offspring inherit from their mother's rank, so stages 2 and 3 should also be separated according to the rank status ($2A$, $2B$ and $3A$, $3B$), but for females only. Indeed, males do not inherit from their mother's rank. Stages 2 and 3 should not be separated according to the maternal experience since macaques from 1 to 3 years are less dependent from their mother and their survival depends less on it (Onishi et al., 2011).

In summary, stage 1 should theoretically be represented by 8 parallel stages (4 per sex) depending on their mother's situation: high-ranking SF ($1A_{SF}$), low-ranking SF ($1B_{SF}$), high-ranking AF ($1A_{AF}$) and low-ranking AF ($1B_{AF}$). Similarly, the stages of juveniles should be each divided into 3 parallel stages: J1 and J2 males (7 and 8), high-ranking J1 and J2 females ($2A$ and $3A$) and low-ranking J1 and J2 females ($2B$ and $3B$).

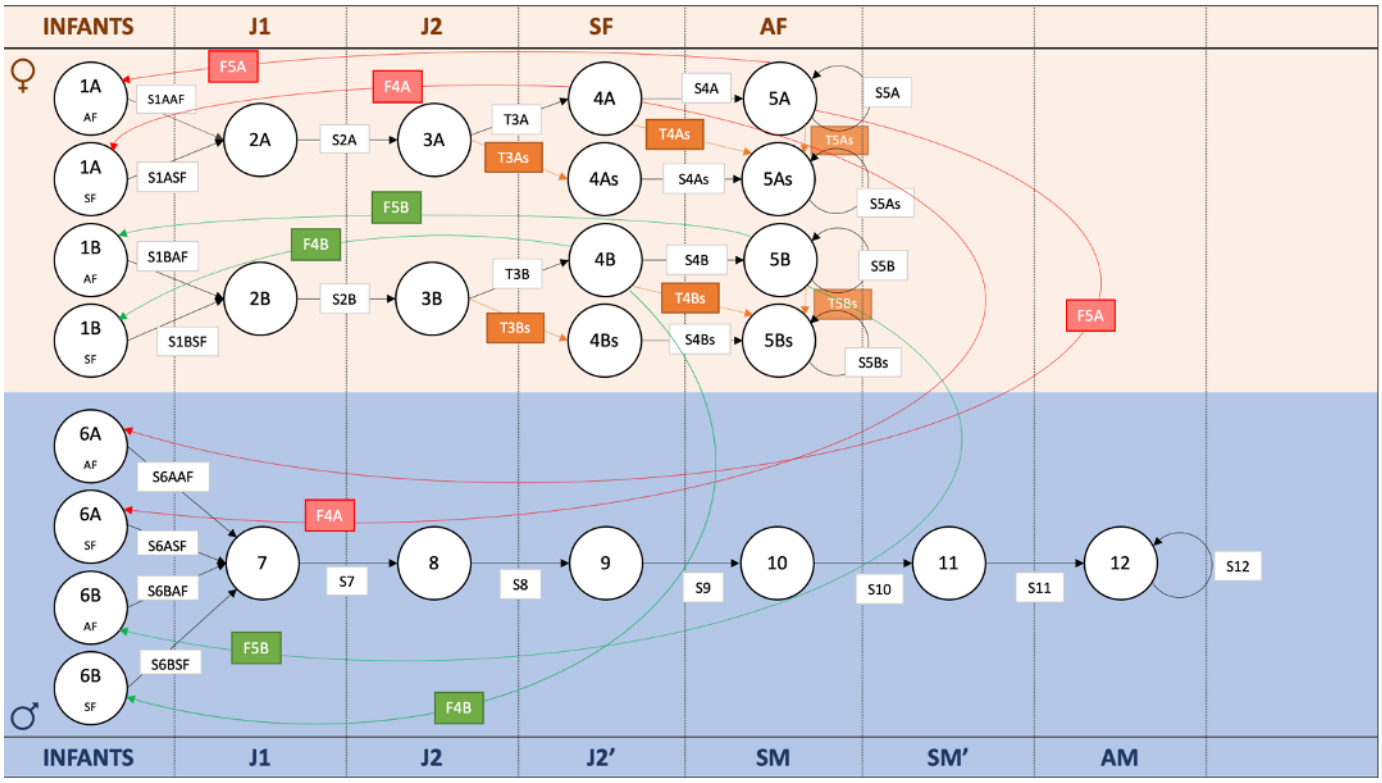


Figure 8: Cycle graph illustrating the complete and theoretical model. The graph is separated between sexes (females in orange background and males in blue background) from birth and considers: the sterile females, the influence of the female rank (A for dominant and B for subordinate) on their own survival and on their offspring survival (with the expectation that survival rates are higher for A than B), the differences in fecundity (represented by curved arrows : A females in green and B females in red) according to the maternal rank where $A > B$, the difference in offspring survival according to the maternal experience ($AF > SF$). Orange arrows are the transitions related to sterilisation (s) (= probability to survive from one stage to the next and probability to be sterilised), T (transition probability) is employed when the transition involves more than one probability.

Stage 4 concerns the subadult females and stage 5 the adult females. The SF and AF differ for their maternal experience. Indeed, a subadult female is systematically nulliparous and an adult female is primi- or multiparous, according to F. Brotcorne's stage identification. As a reminder, infants born from nulliparous mothers are expected to have lower chances of survival than those born from primi- or multiparous females, given the lack of experience of the nulliparous females (Sunderland et al., 2008; Tsuchida et al., 2008). For both SF and AF, the hierarchical status should appear in the model because of their expected differences in both fecundities and survival (high-ranking > low-ranking) (van Noordwijk and van Schaik, 1987). The transitions between SF to AF can only go from a high-ranking SF to a high-ranking AF and a low-ranking SF to a low-ranking AF since the hierarchy is stable over time in a cohort in *M. fascicularis* species (Lane et al., 2010; van Noordwijk and van Schaik, 1999; van Noordwijk and van Schaik, 1987). In addition, the sterile SF ($4As$ and $4Bs$) and AF ($5As$ and $5Bs$) are present in the census data meaning that they should be considered in the model. These sterile females will keep their respective rank, for their differences in survival rates between the rank status. Therefore, both stages 4 and 5 have 4 parallel stages: fertile high- and low-ranking ($4A$, $4B$, $5A$ and $5B$) and sterile high- and low-ranking ($4As$, $4Bs$, $5As$ and $5Bs$).

The last stages concern the males from J2 to adult males (AM). In *M. fasciularis*, males social bonds are also structured on a specific hierarchy from the adolescence (Shively et al., 1985; van Noordwijk and van Schaik, 1985), but it will be ignored in this study for several reasons. First, the male hierarchy is not stable over time (Shively et al., 1985), which complicates the model structure and transitions. Moreover, only the hierarchy of females matters in this context, regarding their important social and structural place into the species socio-ecology and the focus on females fecundities in the birth control context. And third, data about the male hierarchy in the studied population is lacking. One particularity must be highlighted. Males have a slower development than females as they stay 2 years (2-4 years old) as juveniles 2 and 2 years as subadults (4-6 years old) compared to females who stay 1 year in each class. However, the model works on the basis of a step time equal to 1 year. These two classes will be thus divided into two different stages each. Males will consequently have more stages than females where the juveniles 2 stage for males will be divided into J2 (stage 8) and J2' (stage 9) and the subadult stages in SM (stage 10) and SM' (stage 11). In the field, it is impossible to differentiate the "young" J2 from the "old" ones and the "young" SM from the old ones, meaning that census data only count the summed abundance of J2 and SM. Consequently, I will introduce a parameter called *SPLIT*, which will divide the observed number of J2 and SM with a ratio that will be estimated in SAS® (cf. Appendix C).

I will consider a disease outbreak parameter (C), to include the probability of a possible disease outbreak. Including the C parameter allows the estimation of the parameters in normal conditions compared to epidemic conditions that happened in 2012. C will be introduced and estimated from the censuses of year 2012. As cited in Brotcorne's study (2015), only several classes were affected by the *Streptococcus* epidemic. Indeed, mortality rates were 22% for AF, 13.5% for the juveniles and 2.1% for AM in censuses from 2012. These numbers do not mean that the mortality is only due to the epidemic but demonstrate that it impacted the population. Not considering such an epidemic factor in the model would not be correct as the overall survival rates would be overestimated. Introducing a C parameter for the transition from 2011 to 2012 allows to estimate survival probabilities at their nominal rate, multiplied by a constant C that explains the temporary decrease in survival due to the epidemics.

I.2 From the complete model to the reasonable model

Each parameter/stage of the theoretical and complete model at a time was considered with their limitations such as the field reality, the data availability and the data analysis results. In fact, they impose a review of the theoretical model in order to reject some of them and obtain a simplification of the first imagined model, which was too complicated to give reasonable chances of estimating its parameters from available census data. I complete this step first by asking: "What can we afford according to the field and data reality?" (Figure 9). Then, I took into account the results and analyses of the part *Synthesis of collected data* described previously. From these results, I decided which parameters should be conserved and eliminated in the model (called "reasonable model" : Figure 10) before its translation into equations.

a) *First simplifications: field and data limitations*

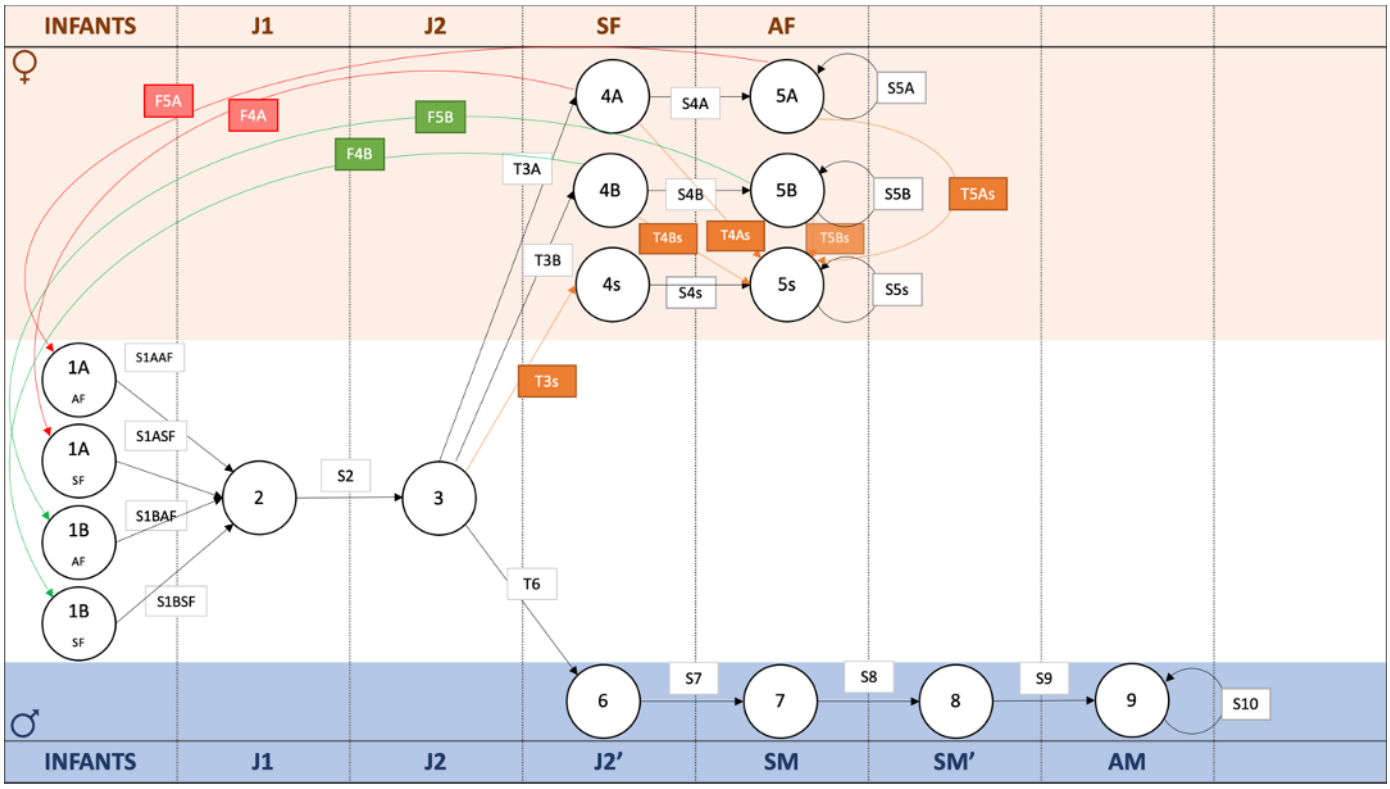


Figure 9: Cycle graph illustrating the first simplifications of the complete model. The graph is separated between sexes (females in orange background and males in blue background) only from the reproductive stages of the females and considers: the influence of the female rank (A for dominant and B for subordinate) on their own survival and on their offspring survival ($A > B$), the differences in fecundity, (curved arrows: A females in green and B females in red) according to the maternal rank where $A > B$, the difference in offspring survival according to the maternal experience ($AF > SF$). Orange arrows are the transitions related to sterilisation (s), involving the probability to survive from one stage to the next as well as the probability to be sterilised. T is employed when the transition involves more than one probability.

First of all, it is impossible to differentiate males and females before they are likely to breed (i.e. subadult, when they show conspicuous secondary sexual characters) in the field during the census data collection. Males and females will be grouped together for stages 1, 2 and 3 and separation will be forced in the model only from stages 4 (SF) and 6 (J2'), by introducing another *SPLIT* parameter (*SPLIT*36), based on a ratio to estimate in SAS® (cf. Appendix C).

As I said before, data on the macaques' histories are available for the Michelin group only. From this data set, I traced the number of infants born to female, established the females' hierarchy, calculated the birth and offspring survival rates for SF and AF and ran statistical analyses. For now, I decided to keep the 4 parallel stages for the infant class, as well as the separation between high and low-ranking SF and AF (Figure 9). I will conclude and readjust these stages according to the statistical results. However, the social network was studied on reproductive females (only AF and some SF) only, no data exists on the rank status of the J1 and J2 female individuals, which forces to group the parallel stages 2A and 2B in one stage 2 and the stages 3A and 3B in one stage 3.

Finally, after reflection I decided to keep the hierarchical status of SF and AF for the fertile females only. The dominance is important mostly because of its influence on fecundity. A sterile female will no longer give infants so taking their rank into account does not coincide with the study objectives and complicates the model. One could ask why I did not keep these two stages for sterile SF and AF anyway to insert a variation of survival between the sterile SF/AF A and sterile SF/AF B. The first reason is that we do not have sufficient data on the females' hierarchy of the population, and too few females were sterilised in the Michelin group to compare their survival rates. Plus, how can we be sure of the variable inducing a difference of survivals between the rank and the sterilisation? We do not have enough hindsight to consider both parameters together for now.

b) *Second simplifications: statistical results*

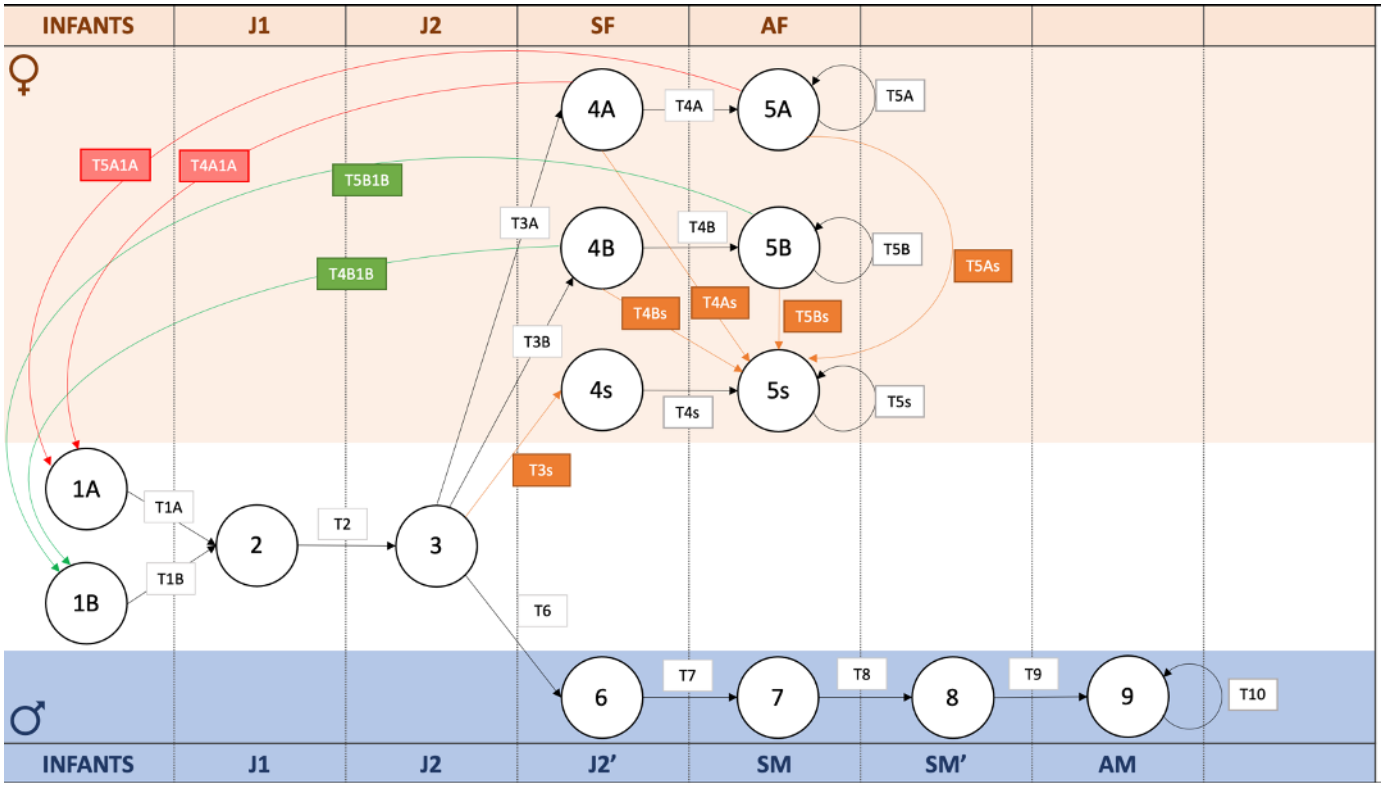


Figure 10: Life cycle graph of the reasonable model, after the second step of simplifications of the complete model. The different stages are represented as circles with the corresponding number (1A, 1B, 2, 3, 4A, 4B, 4s, 5A, 5B, 5s, 6, 7, 8 and 9), and the arrows are the different transition probabilities, named as T. Colors help to read the graph: orange transitions include an annual sterilisation rate, while dark/grey do not, red curves represent transition which include fecundities for the dominant (A) mothers and green ones for subordinate (B) mother.

Data on the maternal experience of Michelin females is a minor estimation, only lasting for 3 years and the follow-up is not enough accurate due to gaps in field observations. In addition, I only have few data about the subadults compared to the adults. Considering the lack of data for the maternal experience, I decided to discard this parameter from the model to reduce the number of parallel stages for infants (Figure 10).

The logistic regression on the effect of rank status on birth and offspring survival did not give any significant results, probably due to a lack of data and hence low statistical power. These results cannot be used in the matrix population model. Nonetheless, I decided to use data from a study about the effect of dominance rank on female lifetime reproductive success in a population of long-tailed macaques in Sumatra (van Noordwijk and van Schaik, 1999). The data set of the latter study included 349 fy and 184 infants over a twelve years period of time, which is statistically more powerful than my data covering only 3 years and comprising less than a third of van Noordwijk's data set.

In their study, van Noordwijk and van Schaik (1999) drew significant conclusions about the effect of female rank on birth rate and offspring survival. They showed that: "*mortality and birth rate combined gave a survival rate of infants until J1 higher for dominant females:* 0.84 *for dominant and* 0.76 *for subordinates*". They added that the larger a group, the higher the influence of rank on offspring survival: survival rate of 0.78 for infants with high-ranking mothers and 0.45 from low-ranking ones. These results lead me to assume that there could be a difference in the survival rate from stage 1 to 2 in the dense population of Ubud but that has not been seen so far. Therefore, I decided to keep each of stages infant, SF and AF split into two parallel stages (1A and 1B, 4A and 4B, 5A and 5B), where a parameter $SPLIT1AB$ (to estimate, cf. Appendix C) will divide the number of infants into 1A and 1B and $RANK$ ($= 0.5$) the number of 4A, 4B and 5A, 5B (see below).

No data from the Michelin group was available on the differences in mortality of dominant females compared to subordinate females. However, van Noordwijk and van Schaik (1999) study teaches the difference between dominant and subordinate females in survival. As cited in their article: "*low-ranking females have a much higher chance of dying during their top-reproductive years than higher-ranking ones, and thus they are more likely to have their reproductive life span cut short*", where top reproductive years are defined as 8-20 years old, which represents the AF. I will issue and test the hypothesis that the difference between survival exists for both SF and AF. To this effect, I will consider the survival rate variation in the model with the expectation that $S4A > S4B$ and that $S5A > S5B$.

I.3 Translation of the reasonable model into equations

Figure 10 shows the life cycle graph of the reasonable model. In Table 5 I define the different transition probabilities (T), which take into account all the probabilities (P) to pass from one stage to the next, that is their respective parameters for each stage of the graph (S and F). Then I give the equations linking the number of individuals in each class for year $t+1$. The proportion of SF or AF successfully sterilised each year is included thanks to $STERILSF$ and $STERILAF$. Finally, the different parameters C ($C2$, $C3$, $C5$, $C9$) will be included in the equations of the respective stages only for year 2012.

Stages	Transitions	Transitions composition	Parameters	Equation
1A	$T4A1A$	$P(\text{give birth } 4A-1A)$	$F4A$	$N_{1A}(t+1) = T4A1A \times N_{4A}(t) + T5A1A \times N_{5A}(t)$
	$T5A1A$	$P(\text{give birth } 5A-1A)$	$F5A$	
1B	$T4B1B$	$P(\text{give birth } 4B-1B)$	$F4B$	$N_{1B}(t+1) = T4B1B \times N_{4B}(t) + T5B1B \times N_{5B}(t)$
	$T5B1B$	$P(\text{give birth } 5B-1B)$	$F5B$	
2	$T1A$	$P(\text{survive } 1A-2)$	$S1A$	$N_2(t+1) = T1A \times N_{1A}(t) + T1B \times N_{1B}(t)$
	$T1B$	$P(\text{survive } 1B-2)$	$S1B$	
3	$T2$	$P(\text{survive } 2-3)$	$S2$	$N_3(t+1) = T2 \times N_2(t)$
4A	$T3A$	$P(\text{survive } 3-4A) \times P(female) \times P(dominant) \times (1-P(\text{sterilized if } SF))$	$S3 \times PF \times RANK \times (1-STERILSF)$	$N_{4A}(t+1) = T3A \times N_3(t)$
4B	$T3B$	$P(\text{survive } 3-4B) \times P(female) \times (1-P(dominant)) \times (1-P(\text{sterilized if } SF))$	$S3 \times PF \times (1-RANK) \times (1-STERILSF)$	$N_{4B}(t+1) = T3B \times N_3(t)$
4s	T3s	$P(\text{survive } 3-4s) \times P(female) \times P(\text{sterilized if } SF)$	$S3 \times PF \times STERILSF$	$N_{4s}(t+1) = T3s \times N_3(t)$
5A	$T4A$	$P(\text{survive } 4A-5A) \times (1-P(\text{sterilized if } AF))$	$S4A \times (1-STERILAF)$	$N_{5A}(t+1) = T4A \times N_{4A}(t) + T5A \times N_{5A}(t)$
	$T5A$	$P(\text{survive } 5A-5A) \times (1-P(\text{sterilized if } AF))$	$S5A \times (1-STERILAF)$	
5B	$T4B$	$P(\text{survive } 4B-5B) \times (1-P(\text{sterilized if } AF))$	$S4B \times (1-STERILAF)$	$N_{5B}(t+1) = T4B \times N_{4B}(t) + T5B \times N_{5B}(t)$
	$T5B$	$P(\text{survive } 5B-5B) \times (1-P(\text{sterilized if } AF))$	$S5B \times (1-STERILAF)$	
5s	$T4s$	$P(\text{survive } 4s-5s)$	$S4s$	$N_{5s}(t+1) = T4s \times N_{4s}(t) + T5s \times N_{5s}(t)$ $+T4As \times N_{4A}(t) + T4Bs \times N_{4B}(t)$ $+T5As \times N_{5A}(t) + T5Bs \times N_{5B}(t)$
	$T5s$	$P(\text{survive } 5s-5s)$	$S5s$	
	$T4As$	$P(\text{survive } 4A-5A) \times P(\text{sterilized if } AF)$	$S4A \times STERILAF$	
	$T4Bs$	$P(\text{survive } 4B-5B) \times P(\text{sterilized if } AF)$	$S4B \times STERILAF$	
	$T5As$	$P(\text{survive } 5A-5A) \times P(\text{sterilized if } AF)$	$S5A \times STERILAF$	
	$T5Bs$	$P(\text{survive } 5B-5B) \times P(\text{sterilized if } AF)$	$S5B \times STERILAF$	
6	$T6$	$P(\text{survive } 3-6) \times P(male)$	$S6 \times (1-PF)$	$N_6(t+1) = T6 \times N_3(t)$
7	$T7$	$P(\text{survive } 6-7)$	$S7$	$N_7(t+1) = T7 \times N_6(t)$
8	$T8$	$P(\text{survive } 7-8)$	$S8$	$N_8(t+1) = T8 \times N_7(t)$
9	$T9$	$P(\text{survive } 8-9)$	$S9$	$N_9(t+1) = T9 \times N_8(t) + T10 \times N_9(t)$
	$T10$	$P(\text{survive } 9-9)$	$S10$	

Table 5: Summary of the different transitions probabilities of the reasonable model and the equations for each stage. $PF = 0.5$, $RANK = 0.5$. $STERILSF = 0$ before 2018 and 0.3871 in 2019. $STERILAF = 0$ before 2017, 2017: $STERILAF = 0.07373$, 2018: $STERILAF = 0.0873$, 2019: $STERILAF = 0.2037$.

II From the reasonable model to the final model: estimations and simplifications

II.1 General approach

This approach comprises two main objectives, which are the estimation of the parameters and the simplification of the reasonable model until the final model. The general principle is to estimate the parameters of the model by reaching the best price-quality ratio. In other words, the goal is to conserve the parameters (and only these) significantly enhancing the model quality, that is its explanation of the data or its goodness of fit.

Parameter estimates are generated from the census data on the basis of the minimisation of an objective function, the residual sum of squares (RSS), i.e. the sum over all observations (couples of years) and all model stages of the difference between the observed and predicted numbers of individuals. This was achieved by the NLP (Non-Linear Programming) procedure of SAS® which contains several optimisation approaches and can employ a large range of algorithms for minimising or maximising a continuous nonlinear function. It also allows for constriction of parameters in different ways such as among others upper and lower boundaries or linear limitations (SAS-Institute-Inc., 2014).

The model simplification consists in the suppression of the potential effects that are not explained by the data set. Such simplifications entail equalities (or absence of difference) between some parameters or suppression of parameters when necessary. They should start with the parameters of least interest since statistical power to test for effects increases as the model number of parameters is reduced. Consequently, the simplification is sequential and requires a logical way of thinking. Here, the notion of priority for the parameter conservation is primordial and the decision to remove a specific parameter needs to be based on theoretical knowledge of the species' demographic properties. Model simplification and decisions are based on the Akaike Information Criterion (*AIC*) and the corrected version of the *AIC* (AIC_c), which quantifies the price-quality ratio of the model to explain the data. When considering several models, the selected model is the one having the lowest *AIC* or AIC_c values computed with the following formulas:

$$AIC = 2k + n \times \ln(RSS)$$

$$AIC_c = AIC + \frac{2k \times (k+1)}{n-k-1}$$

Where k is the number of parameters included in the model to estimate and n is the sample size.

AIC rests upon a compromise between the goodness of fit (quality) and the model complexity (price). It penalises models having numerous parameters and thus limits over-fitting, which is required since augmenting the number of parameters necessarily enhances the goodness of fit. AIC_c is recommended when models are based on small samples and/or have many parameters. Actually, it considers a supplementary penalty for the additional parameters, preventing overfitting for small datasets (Burnham et al., 2002).

In practice, the system of equations of Table 5 was implemented in SAS®, with the parameters to estimate, their respective estimation constraints and the objective function. NLP procedure translated the equations into the corresponding age-structured matrix (Leslie matrix) to give the estimations with the minimisation of the RSS. Before selecting the model describing the data at best, I verified the estimation quality to prevent any risk of a local minimum during optimisation, which is recommended especially when a model is based on few data and contains many parameters to estimate. For more details, please refer to Appendix C.

II.2 Parameter estimates and reasonable model simplification

Because there is a large number of submodels possible, created by removing one or several parameters from the start model, it is practically unfeasible to test all possible submodels, although this would have been the best strategy to find the most suitable model if it was possible. Therefore, I used a sequential model simplification approach, simplifying the model and keeping it as a new start model for the next simplification model when the *AICc* was lower, discarding it when the *AICc* was higher. The risk of such a sequential approach being that the outcome may depend on the path taken, which is partly defined by more or less subjective choices about the priority order accorded by the programmer. I personally tried two ways of simplification. The first one begins with the simplification of the *C* parameters, continues with the survivals of males and juveniles, and ends with female parameters, as *C* and male/juvenile parameters are of lower interest compared to the parameters related to female reproductive success. However, during this first attempt, I realised that bias in parameter estimation was mainly due to the distinction between high- and low-ranking stages. This is why I tried another way of simplification which begins with the male/juvenile survivals, continues with the differences between A and B and finally with parameter *C*. Thus, the given priority order is different between path of simplification 1 and 2. However, the logic of simplification is the same in both procedures and actually led to the same results. Justifications are hence similar for each procedure (or path).

The first estimations of the reasonable model parameters gave many aberrant results, such as parameters stuck to the initial value or the upper (1) or lower boundaries (0), which is biologically and demographically unlikely. This shows that, when confronting the model to the data, bias was generated, and NLP procedure could not estimate the parameters properly, indicating that an important simplification was necessary. Indeed, the reasonable model includes a lot of parameters to estimate from a relatively small data set. Appendix D shows the detailed justifications of the model simplifications, which are the same for both simplification paths.

In long-tailed macaques males leave the social group as soon as they are pubescent (±4 years old), which confronts them to threats such as competition with other males mainly for mating with reproductive females. Consequently, it is logical to assume that their survival depends on their age, since hormonal changes and aggressiveness also depend on their age (Lane et al., 2010; van Noordwijk and van Schaik, 1987). Even though it is biologically reasonable to suppose that the survival between J2 and J2', as well as young SM and old SM are different, our data set does not allow to significantly distinguish these survivals, justifying a simplification from four to two parameters.

The final model (Equation 5) considers a unique survival rate for all females ($S4$ for stages $S4A$, $S4B$, $S4s$, $S5A$, $S5B$, $S5s$) and one for SM and AM ($S8$). $S5A$, $S5B$, $S5s$ and $S10$ were always overestimated. This is due to the particularity of the adult stages, which are continuously refilled. Actually, stages 5s, 5A, 5B and 10 contain both individuals going from the subadult to the adult stage and the adults remaining adults until death, depending on survival of both the adolescents and the adults. With this sample, the model parameter optimisation algorithm was not able to single out the precise number of individuals going from SF/SM' to AF/AM the following year. But, this is not a structural problem because, with enough data, the algorithm should be able to distinguish the different parameters. Also, we did not notice an over-mortality in sterilised females since the first sterilisation campaigns. Hence, we can assume that the survival rate of sterile females is not significantly different from the one of fertile females.

None of the statistical analyses provided significant results proving the existence of a difference in reproductive success between high-ranked and low-ranked females. The implementation of these differences into the model was based on assumptions and theoretical knowledge from a study on another population (van Noordwijk and van Schaik, 1999). Including such differences was therefore risky but also a way to test if they could exist or not. The simplifications occurred on the infants survivals and the SF fecundities and survivals and the AF fecundities and survivals. The results indicate that for now, the data set does not allow to consider a difference in high- and low-ranking females. Indeed, regrouping stages 1A and 1B into one stage 1, 4A and 4B into one stage 4 and 5A and 5B into one stage 5 allowed the reduction of the model complexity, and improved its goodness of fit.

Finally, by assuming the absence of difference between fecundities of SF and AF, the model is simpler while not losing much in terms of quality, as the *AIC* value decreases: it is a better compromise.

In conclusion, among all candidate models, the best one (Equation 5) (i.e. the one presenting the best cost effectiveness in fitting to the data quantified by set the most adequately its lowest *AICc* score) has an RSS of 42663.61 and includes 10 parameters, which in turn gives an *AICc* score of 530.742. This model is the best model selected via the two paths of model simplification, which leads to two important conclusions: (*1*) the end result seems robust to the sequential path used in model simplification, and (*2*) the optimisation algorithm was successful in finding the best parameter estimates. Comparatively, the reasonable model comprised 27 parameters and its *AICc* was equal to 582.293. The final model is fairly simpler than the reasonable model, as it does not consider any difference between the high- and low-ranking females and includes only one fertility rate and one survival rate for all females past the age of 4. The computation of the *AICc* proved that the model benefits from the absence of these differences and their related parameters. This

confirms that the data set does not give enough significant indications on the existence of such differences between high- and low-ranking individuals. Either these differences exist but there is not enough data to prove it yet, or they do not exist, but it is impossible to know this for now.

$$\begin{pmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \\ N_{4s}(t) \\ N_5(t) \\ N_{5s}(t) \\ N_6(t) \\ N_7(t) \\ N_8(t) \\ N_9(t) \end{pmatrix} \times \begin{pmatrix} 0 & 0 & 0 & F5 & 0 & F5 & 0 & 0 & 0 & 0 & 0 \\ S1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S3 \times PF \times (1-STERIL) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S3 \times PF \times STERIL & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S4 \times (1-STERIL) & 0 & S4 \times (1-STERIL) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S4 \times STERIL & S4 & S4 \times STERIL & S4 & 0 & 0 & 0 & 0 \\ 0 & 0 & S6 \times (1-PF) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S8 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S8 & S8 \end{pmatrix} = \begin{pmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ N_4(t+1) \\ N_{4s}(t+1) \\ N_5(t+1) \\ N_{5s}(t+1) \\ N_6(t+1) \\ N_7(t+1) \\ N_8(t+1) \\ N_9(t+1) \end{pmatrix} \quad (5)$$

MODEL INTERPRETATION AND UTILISATION

I Parameter estimates and interpretations

Table 6 shows the values of the estimated parameters for the final model selected with their Profile Likelihood Based Confidence Intervals considering a significance level (α) of 5%. These limits indicate the standard errors of the estimations of the parameters. Using such intervals is very important when programming from small data set. Actually, the maximum likelihood estimate of poor samples does not always follow a normal distribution.

Parameter	Estimate	Profile likelihood confidence limits
$F5$	0.506132	[0.500390; 0.511882]
$S1$	0.907624	[0.895947; 0.919324]
$S2$	0.940685	[0.917904; 0.964116]
$S3$	0.557807	[0.523025; 0.593541]
$S4$	0.914550	[0.909716; 0.919375]
$S6$	0.849147	[0.814709; 0.882181]
$S8$	0.764125	[0.746651; 0.781262]
$SPLIT36$	0.661787	[0.637168; 0.685351]
$SPLIT78$	0.315734	[0.260112; 0.369291]

Table 6: Parameters estimates with their respective profile likelihood confidence limits.

The majority of survival rates is close to 0.9, except for $S3$ and $S8$. Such results are close to what was expected, given the knowledge of the species, and they illustrate the important growth of the population. Yet, survival parameters could be mis-estimated because of bias coming from the census data itself, where some counts have been overestimated some years and others underestimated. For instance, in Table 2 we can see a higher number of J1 in 2019 compared to the number of infants in 2018, which is demographically impossible. It indicates that either the number of infants was underestimated or the number of J1 was overestimated. With such observed data, the survival will automatically be overestimated. Indeed, the survival explaining this particular transition at best would be equal to 1 (and even > 1 if it was not constrained). $S4$ should be the most accurate estimation, since it is involved in many equations (stages 4, 4s, 5 and 5s).

The value of $S3$ is very low, which is peculiar and unlikely. The reason of this low value is unknown, but we can suppose that bias is generated by stage J2 which takes into account many individuals compared to SF. Indeed, it considers all J2 observed in the field, that is females and males J2. Moreover, the software has three information: the number of J2 at year t, the number of SF and SM at year $t+1$, from which it estimates four parameters: $S3$, $S6$, $SPLIT36$ and $SPLIT78$. It is therefore probable that the estimation of $S3$ is lowered due to the small number of SF compared to the number of SM (which encompasses a period of two years). We can also suppose that the sex ratio $(50:50)$ forced in the equation of stages 6 and 3 is not appropriate, since males migrate and are subjected to more threats than females when leaving the group before or during puberty. Moreover, males are likely to be involved in more aggressive interactions, sometimes lethal, within their group than females. We could reasonably imagine that the sex ratio of J2 as a whole is higher, with more females than males. It is also likely that $S3$ is low because of the high number of females (SF and AF together). Maybe the way to fit the data the most properly is to lower the value of $S3$ (due to the high value of $S4$)? Similarly, as J2 stage is supplied by the number of J1, $S2$ could be overestimated because of the high number of J2 compared to J1, and hence could lower $S3$ value.

There is a difference in survivals between the reproductive males and females, which is confirmed by the mean sex ratio of the population where on average there are three females for 1 male (cf. Cloutier et al., 2018). Such results are consistent with the biological, ethological and ecological differences between males and females. Indeed, males are supposed to face higher risks of mortality because of their migrations and generally speaking males in primates have a lower lifespan than females.

The fecundity rate given for the SF and AF is estimated at 0.51, which is realistic regarding the birth-interval rate of females in *Macaca fasciularis*. Indeed, females give birth to approximately one offspring every two years (van Noordwijk and van Schaik, 1999; van Noordwijk and van Schaik, 1987).

With these values, we can construct the projection matrix which summarizes all the transition probabilities (Equation 5). The matrix is useful afterwards to run projections of the population to *(i)* compare the observed data and predicted data, *(ii)* project the population over several years under different scenarios.

II Comparison between observed data and predicted data

It is essential to check the precision of the estimated parameters. I will compare the evolution of the population from 2009 to 2020 from the data censuses (Table 2 : observed data) and the evolution of the population from 2009 to 2020 from the initial population size of 2009 and with the projection matrix of Equation 5 (predicted data). To compute the predicted abundances, I will consider the temporal variability in the model structure and parameters as implemented: (*1*) sterile stages exist only from 2016-2017, (*2*) sterilisation probabilities were different from 2017 to 2019, and (*3*) the epidemic outbreak (modelled by the C parameter) occurred in 2011-2012.

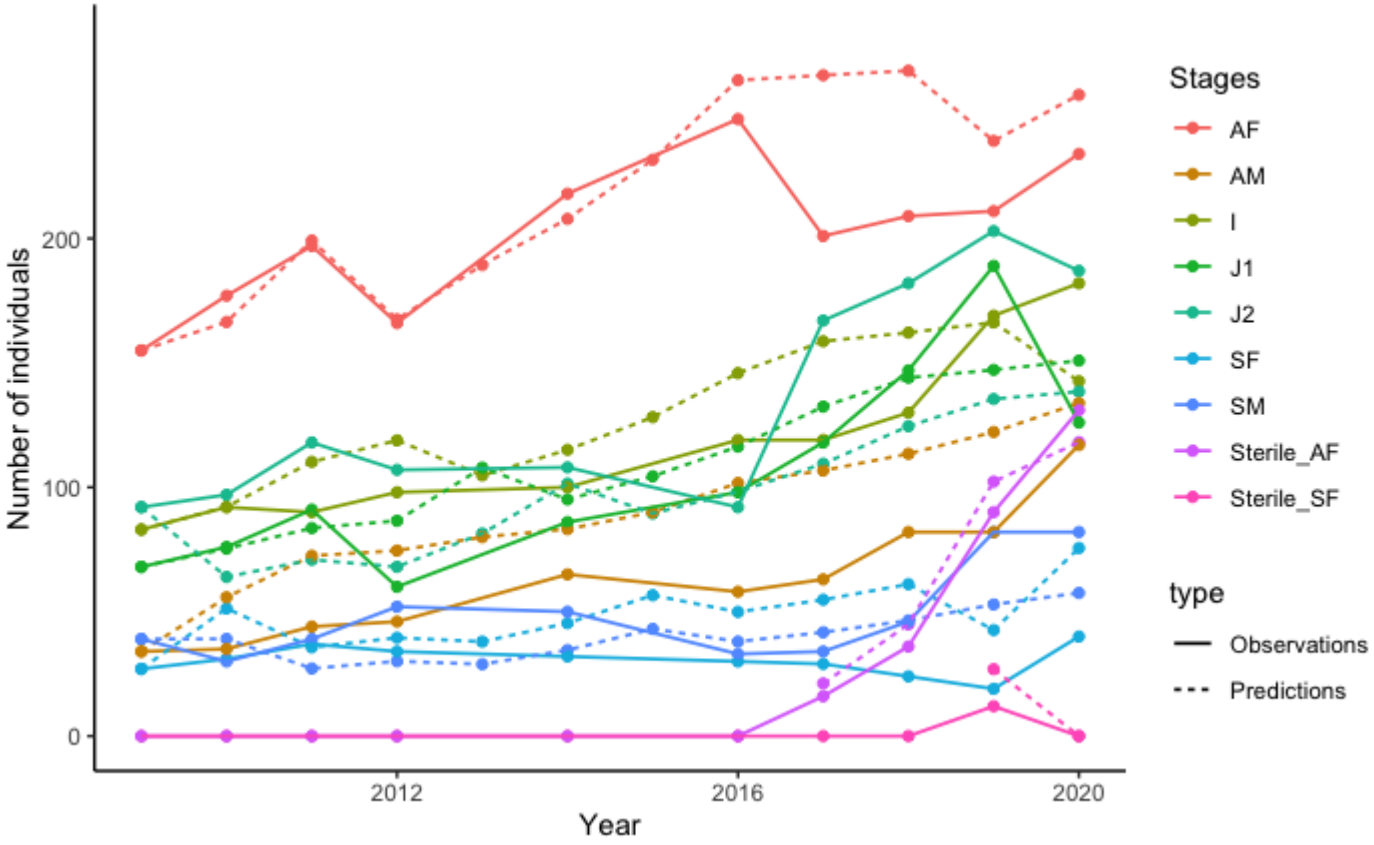


Figure 11: Graph representing the evolution of the population for each stage between 2009 and 2020 from observed data (full lines) and from predicted data (dotted lines).

As we can see on Figure 11, the predicted data sticks reasonably to the reality, although it confirms that some parameters were over or underestimated. The graph does not show any underestimation for $S3$ and $S1$, $S2$, $S4$, and $S8$ looks overestimated. The fecundity $F5$ looks a bit overestimated too, as we can see the number of infants predicted is almost all the time greater than the observed data.

III Projections and stochasticity analyses

III.1 Sensitivity and elasticity analyses

The package *popbio* in R® (Stubben et al., 2007) allows different analyses from the matrix projection, including the estimation of λ, sensitivity and elasticity analyses, as well as running different projections under various scenarios.

Sensitivity and elasticity are largely employed for analysing projection matrices, as these tests aim at estimating the selection pressures affecting the demographic parameters. The principle of such analyses rests upon evaluating how sensitive λ is (sensitivity) to absolute changes, as small as they are, and one at a time, of the model parameters. Elasticity is almost identical to sensitivity except that it is expressed as a logarithmic function, where elasticities of the projection matrix sum to 1 and each parameter elasticity is expressed as a proportion and non-dimensionally. Thereby, we can compare and understand directly and easily the contribution of each parameter to the λ and see on which parameters it is necessary to work in order to vary the λ (Alberts et al., 2003; Carslake et al., 2009; Caswell, 2001; Crouse et al., 1987).

In a basic scenario where the environmental conditions remain as they presently are and where no sterilisation occur in the next few years, the projection matrix considers only the sterile AF (no sterile SF) already present in the population and does not consider any future sterilisation rate. The sensitivity and elasticity analyses of this projection matrix indicate a $\lambda = 1.10$, which means that every year, the population would increase by 10%. Also, the analyses point out that an increase in $S4$ for AF has a greater impact on the population growth rate than the same proportional change in any other vital rate. Indeed, a 1% change in $S4$ will increase λ by 0.46%, whereas a 1% change in $F5$ will increase λ by only 0.02% for SF and 0.09% for AF. If we consider the C parameter into the projection matrix, then $\lambda = 0.93$. In addition, a change of 1% in $S4$ will increase λ by 0.34%, but a change 1% in $F5$ will increase λ by only 0.03% in SF and 0.1% for AF.

Consequently, the best way to reach $\lambda = 1$ for Ubud population would be through diminishing the survival rate of AF. Nonetheless, culling or moving any animals is prohibited. The only way to act on λ is therefore through diminishing F or augmenting the sterilisation rate, which reduces the transitions probability of fertile AF and SF and augments the one of sterile AF and SF. Eventually implementing an annual sterilisation rate or sterilising a proportion of females every few years would have the same impact on the population growth rate than acting on $S4$.

III.2 Projections

The population control program aims at stabilising the population size, which is not reached yet ($\lambda > 1$). This means that other sterilisation campaigns will be necessary. The sterilisation rate suggested before the first campaigns was of 52%. Here, I will attempt to assess a new sterilisation rate allowing to reach a $\lambda = 1$ firstly in a purely deterministic way and secondly considering sources of stochasticity in population dynamics. Different types of scenarios, deterministic and stochastic, will be studied and the population will be projected over 25 years. It is important to keep in mind that the projections are based on estimated parameters (vital rates) illustrating the population reality. These parameters can have some biases even though they are based on the reality, and in the reality they can vary over time (e.g. according to environmental conditions). It is therefore important to interpret the results with a step back and to remain cautious before drawing any conclusion.

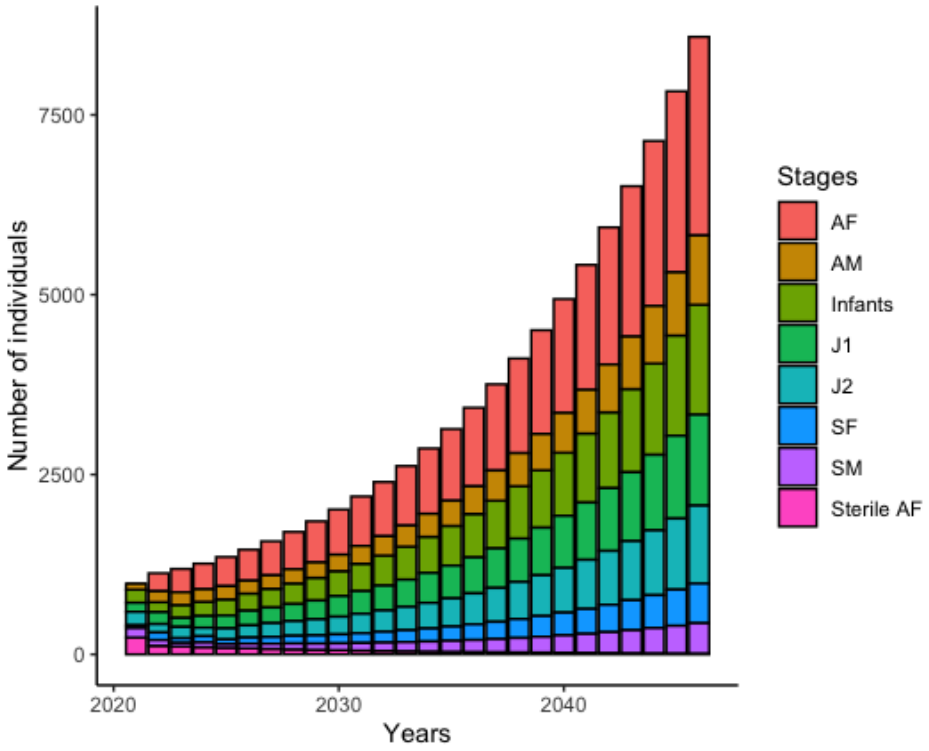
a) *Deterministic projections*

The population was projected without any temporal variability (no epidemic) under two scenarios : (a) without new sterilisation; (b) with sterilisation every year.

As we can see on the graphs of Figure 12 , if no epidemic outbreak occurs, if the current environmental conditions remain unchanged, and if there are no sterilisation campaigns in the future, the population will not cease growing (Figure 12a). Even so this projection is purely theoretical without assuming any retroactive effect of density-dependence which should occur because N should eventually approach the carrying capacity of the environment. By implementing the same sterilisation rate than between 2017 and 2019 (mean sterilisation rate of 0.19) each year, the population should stabilise in a first time and then reduce in size from 2030 ($\lambda = 0.96$) (Figure 12b).

Such scenarios are an illustration of what could happen to the population under some circumstances, indicating the turnover of the population. Yet these two projections are deterministic and do not suppose any stochastic events, which is virtually impossible. Such stochastic events are for instance epidemic outbreaks (density-dependance) which can induce variations in vital rates. Moreover, maintaining a sterilisation rate over the years is difficult regarding the time and budget needed in the field.

(a) Deterministic projection of the population over 25 years without sterilisation



(b) Deterministic projection of the population over 25 years with sterilisations

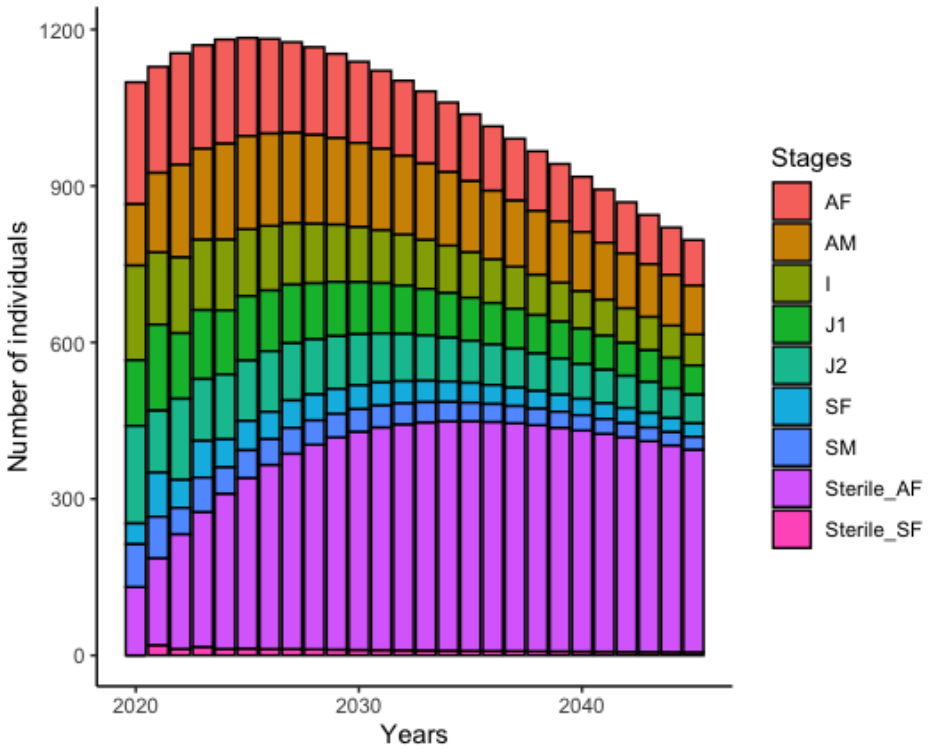


Figure 12: Deterministic projections from 2020 to 2045: (a) Without sterilisation campaigns ($\lambda = 1.097$); (b) With a sterilisation rate of 0.19 every year ($\lambda = 0.962$).

b) *Stochastic projections*

In a second time, I tested the sensitivity of λ ($\bar{\lambda}$ over 25 years projections) to the frequency of epidemic outbreaks (from every 6 years to every 18 years) and the sterilisation rate (0 to 0.7). Note that if the population is facing an epidemic, I assume that no sterilisation campaign occurs. As we can see on the chart (Figure 13), λ decreases linearly with both the epidemic frequency and sterilisation rate, which supports the basic concepts in population biology (Introduction: section II). Indeed, epidemic outbreaks are density-dependent factors, and sterilisation can also be considered as a density-dependent factor: while one tends to reduce the survivals the other lowers the birth rates, which eventually leads to a decrease in the population density and hence in the mean population growth rate (λ).

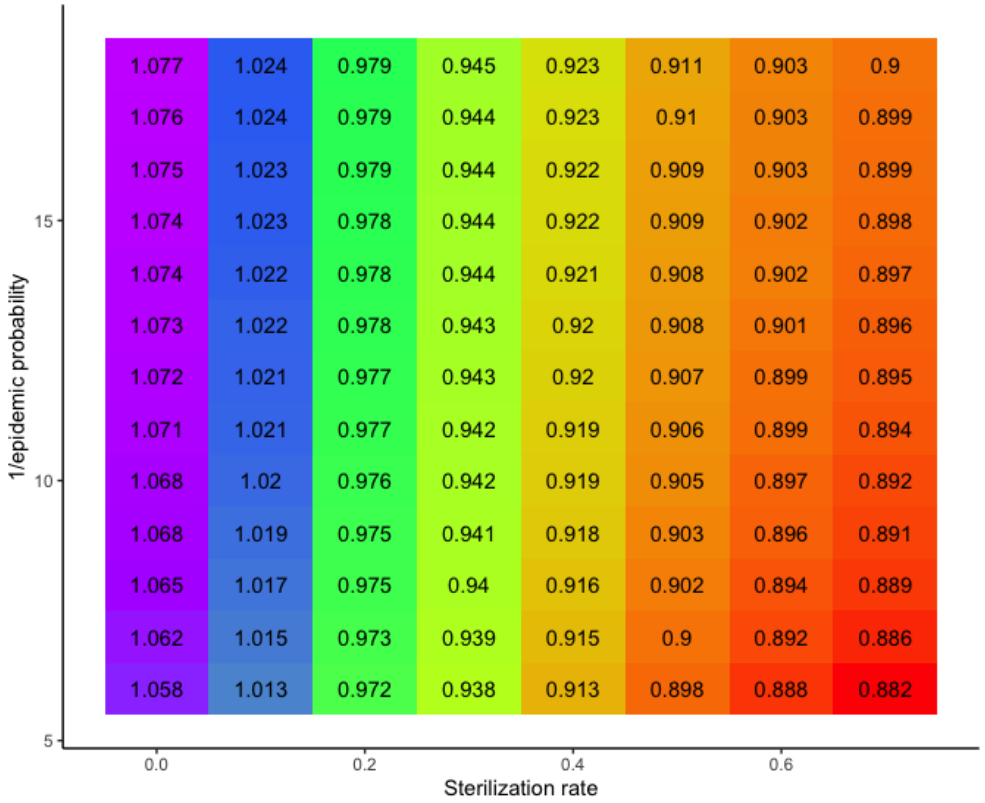


Figure 13: Sensitivity of lambda to the epidemic outbreak probability of frequency (in years) and sterilisation rate. The y axis is the probability of occurrence of the epidemic: from every 6 years to once every 18 years; the x axis is the annual probability of sterilisation (0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7) every year. The colored values are the mean lambda over 1000 simulations for 25 years projections.

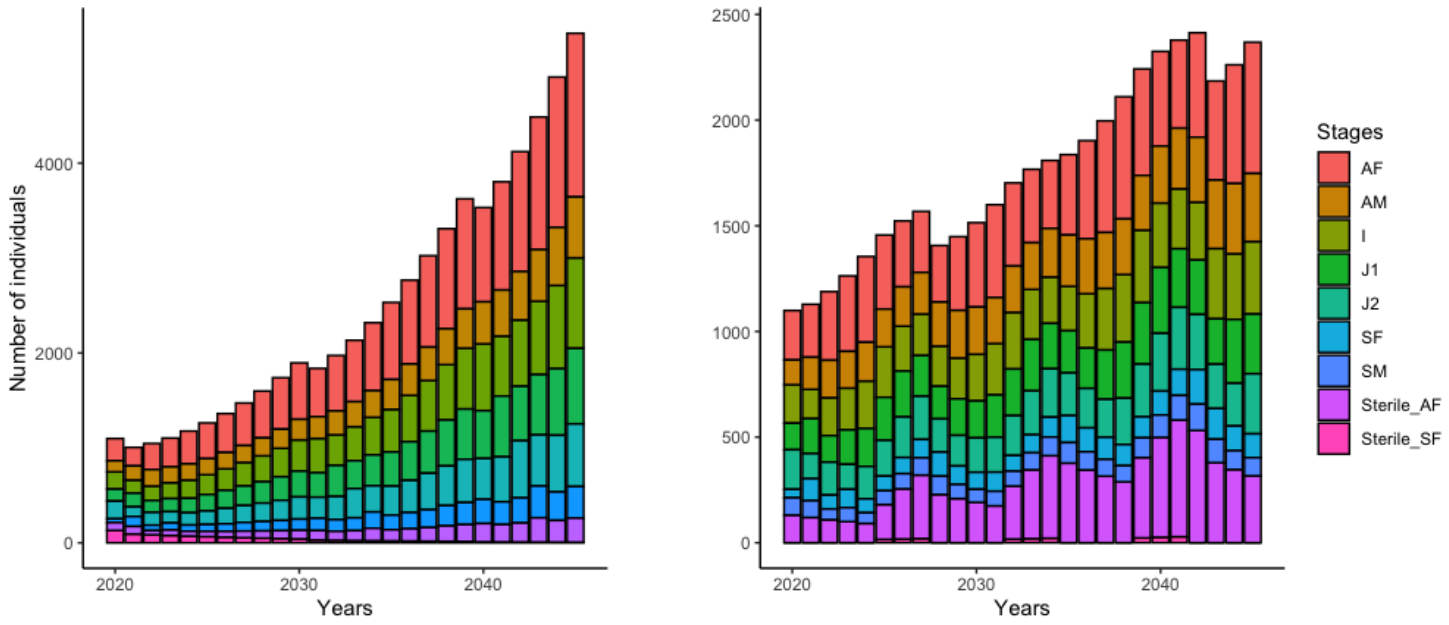
Finally, I will make the assumption that *Streptococcus* epidemic outbreaks occur every 18 years (Brotcorne, Maslarov, et al., 2014) by inserting a probability of $1/18$ for C parameters and will compute different sterilisation scenarios. Figure 14 illustrates the population size evolution over 25 years under four different scenarios, that are summarised in Table 7. The first scenario (*Scenario a)*) is the case where no sterilisation occurs from 2020. As we can see on the chart on Figure 14a, the population will not stop growing which confirms that more reproductive females should be sterilised. In *Scenario b)* however, the population still increases in size but more steadily (Figure 14b) while in *Scenario c)*, it decreases relatively more sharply, which indicates a quasi-stability (Figure 14c). Lastly, it is practically impossible to sterilise 50% of the females in one go in the field. We must spread the sterilisation campaigns over several years. The last sterilisation campaigns were spread over 3 years and, during only year 2019, approximately 30% of reproductive females were sterilised. Therefore, we can assume that it is realisable to sterilise 25% of the reproductive females in one year, and apply this sterilisation rate every year during 4 consecutive years (*Scenario d)*). Among all tested scenarios, the latter is the more realistic and closer to the objective (Figure 14d).

Scnenarios	**Epidemic probability**	**Sterilisation rate**	λ	**Frequency of sterilisation (every x years)**	**Consecutive years of sterilisation**	$\bar{\lambda}$
Scenario a)	0.05556	0	1.07	/	/	1.07
Scenario b)	0.05556	0.19	0.96	4	3	1.04
Scenario c)	0.05556	0.5	0.76	4	1	0.99
Scenario d)	0.05556	0.25	0.92	4	4	1.005

Table 7: Summary of the evolution of the population over 25 years under 4 different sterilisation scenarios and with epidemic outbreak, referring to Figure 14. From left to right : the four scenarios, probability of epidemic outbreak ($1/18$), Sterilisation rate applied at each sterilisation campaign (one campaign per year), λ of the Leslie matrix when sterilisation occurs, Frequency of the sterilisation campaigns (every x years), Consecutive years of sterilisation campaigns where the sterilisation rate is applied, Mean λ over 25 years.

(a) Stochastic projection without sterilisation

(b) Stochastic projection with annual sterilisation (19%) over 3 years and every 4 years



(c) Stochastic projection with spontaneous sterilisation (50%) every 4 years

(d) Stochastic projection with annual sterilisation (25%) over 4 years and every 3 years.

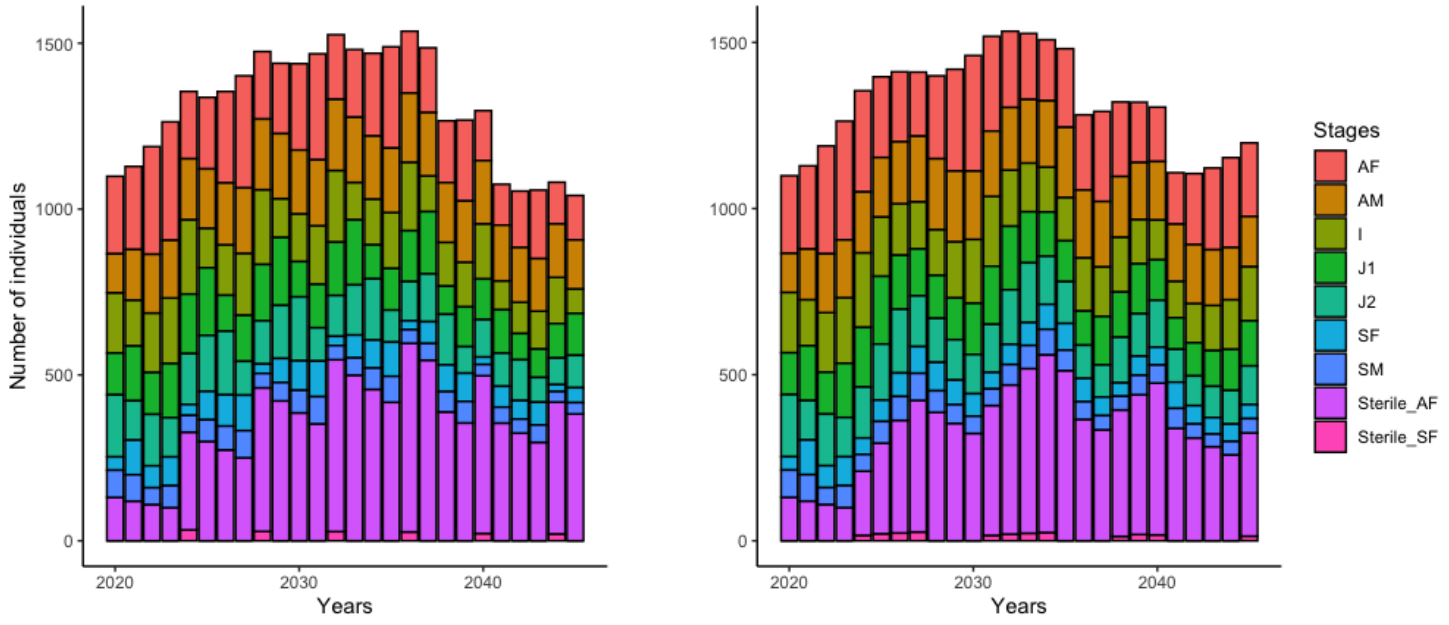


Figure 14: Stochastic projections under different scenarios.

DISCUSSION AND PERSPECTIVES

Given the fact that I chose to describe methods and discuss results together for each of the main steps of my work one after the other (instead of a classical "material and methods then results" structure), I will build the discussion in a more general perspective with integrative results.

First and foremost, the demographic data collected between 2017 and 2020 including those related to the sterilisations were successfully integrated into the demographic model. The numbers of sterilised reproductive females, the sterilisation rates and the respective vital rates were directly implemented by adding new stages and parameters to the previous model.

Among all biological parameters that could be considered for the Ubud population modelling, two types of ethological data were retained: the maternal experience and the hierarchical status of the reproductive females, supposed to impact their reproductive success. The hypothesis of a difference in reproductive success according to rank status is still controversial since some studies describing such correlation provided significant results (Altmann et al., 2005; Borries et al., 1991; Drickamer, 1974; Pusey et al., 1997; van Noordwijk and van Schaik, 1999; Wasser et al., 2004) while others did not (Berman, 1988; Gouzoules et al., 1982; Paul et al., 1990; Takahata et al., 1999; van Noordwijk and van Schaik, 1999; Wolfe, 1984). As for the Ubud population, the results on the relationship between the social rank and the reproductive success was not significant. Such results indicate that there is either a well-established and true difference among females, but the data set is not sufficient to notice it, or, that there is no difference in reality. Concerning the maternal experience, the data set was too poor to test any hypothesis, which lets the question pending. Further ethological observations on the Michelin group should follow in the near future in order to get weightier (in number and duration) data sets and (re)test the hypotheses, with a more rigorous data collection in the field. In fact, due to field constraints, there were many missing values and uncertainties in the follow-up data set of the Michelin group. Those were due to gaps in the follow-up period and irregularities of field missions and/or the difficulty to collect neat and systematic follow-up data in such large groups of primates. For instance, following the challenges to identify such a large number of individuals, data was collected on known individuals only and when events (pregnancy, fight, death, birth...) happened to them and could be noticed, which resulted in missing observations for sometimes long periods of time. With such a technique, it is impossible to know if the missing value is due to a disappearance or if the animal was not observed, or if the animal was observed but nothing "important" happened to him. To overcome this issue, it would be necessary to systematically conduct a demographical follow-up at least once a month for every known individual and to take note even if nothing important happened, which would allow to prevent

some uncertainties. Because my data set lacked statistical power, I chose to include in the model results of the study of van Noordwijk and van Schaik (1999) which had more statistical power (but does not allow to control for inter-population variability in ecological and demographical conditions). Nevertheless, the final model did not consider any difference in reproductive success between high and low-ranking females due to bias generated by the separation of individuals according to their rank. Therefore, if we want to test if the social rank influences females and offspring vital rates and thus the population demography, it is necessary to improve the data set quantity and quality.

The values of the final model parameters were relatively well fitting to the population reality although $S3$ value was unexpected indicating estimations problems which can be due to several reasons. First, bias is probably generated by the merged stages in the field (nobs36) that are split during modelling (nobs3 and nobs6): stage 3 is supplied by stage 2 and stage 6 itself, where males stay longer as J2 than females, which induce the algorithm to overestimate $S2$ and underestimate $S3$. Then, there could be an imbalance between $S2$ and $S4$: the only way for the model to stick to the data is through reducing $S3$ given the high values of $S2$ and $S4$. Finally, estimation problems could likely originate from the data set itself. The census data set (Table 2) includes some peculiarities. Particularly, as we can see on the chart of Figure 11, major problems occur between 2016 and 2017, where the number of individuals (especially J2 and J1) augmented drastically in a year, which is demographically impossible, while the number of SF is quasi stable over the years and the number of AF decreases. It seems likely that from 2016 to 2017, there could have been some mistakes during the counting in the field. Counting such large groups of macaques is very challenging and require several observers at the same time given the low cohesiveness of the groups. Despite the inter-observer reliability tests conducted to ensure a consistency in age/sex class identification, the low visibility conditions at dawn and the rapidity of the macaque movement during travelling induce a range of identification errors. Despite the multiplication of the census to reach the most real average number of individuals in each class, a risk of error persists. The census method should be better calibrated to improve the data in the future, for instance, by using alternative census methods such as capture/recapture technique if possible. Hence, such bias into the next census could be prevented. For what happens next, it would be worth removing year 2016 from the census data (which involves slight modifications of the SAS® script due to a gap of 3 years between 2014 and 2017 that would appear in the data set) to see if this removal improves the parameter estimates and have a better understanding of the bias generated by the data set.

Generally speaking, my final model is not that much more complicated than the model of Fanny Cloutier (Cloutier et al., 2018). The only differences are the new stages included for sterilised individuals and the supplementary 4 years of observations, which should improve the estimations by the algorithm. Therefore, I did not expect big differences in the parameter estimations between my model and the previous one. My results are close to hers for all parameters except for the values of $S1$, $S3$ (see above) and $F5$. In F. Cloutier's model, $S1$ was estimated at 0.84 while mine was estimated at 0.91. This difference is actually explained by the new observed data: the number of infants and J1 augmented quite sharply between 2017 and 2020 in the observed data (Figure 11), which increases the value estimated for $S1$, compared to between 2009 and 2016 where these numbers followed a lower trend. F. Cloutier could see a difference in fecundity between SF and AF ($F4 = 0.69$ and $F5 = 0.41$). I personally simplified those into one parameter: $F5 = 0.51$, which

is approximately halfway between $F4$ and $F5$ of F. Cloutier's values. Regarding the number of infants progressively increasing from 2009 to 2020, the value of the fecundity is expected to be higher for my model than for the one of F. Cloutier's, which is actually the case. Finally, the estimated values of male survivals are a bit more elevated (of some tenths) for my model, which corresponds to the population reality regarding the higher number of males from 2017 to 2020.

The overall elevated values of survival rates over the years illustrate the important growth of the population of Ubud. Indeed, regarding the daily provisioning of the macaques into the Monkey Forest, animals experience health, survival and reproduction enhancement (Asquith, 1989; van Noordwijk and van Schaik, 1999; van Noordwijk and van Schaik, 1987; Whitten, 1983). Particularly for males, which migrate less in case of overcrowding and stay longer in their natal group, reducing some hazards and increasing their survival (Lane et al., 2010). Also, it is possible that the population faces an important growth because it has recovered from the epidemic outbreak of 2012. Therefore, in terms of population management, efforts should be undertaken for two types of resources: food and space. In fact, by drastically reducing food provisioning, the population should stabilise naturally given the density dependence following competition for food. The lack of space then forces monkeys to congregate and brings them closer to villages and touristic infrastructures, which intensifies the conflicts with humans. If the monkeys had more natural habitat and forest food resources, they could range in larger areas and further from humans to have more human-independent lives. In turn, competition and predation should increase and would regulate the population density (mortality should increase and/or fecundity should decrease). Although all of this is well known by the local and Belgian teams, it remains difficult to implement such actions and the staff of the Ubud Monkey Forest is reluctant to stop monkey provisioning for two main reasons. First, because the presence of the monkeys inside the Forest Sanctuary attracts many tourists and represents a great economic opportunity, and second, because the daily provisioning is a control strategy to keep macaques inside the forest and avoid conflicts with neighbouring communities. Moreover, tourism is increasingly present in Bali and leads to a landscape anthropisation reducing natural habitat areas. Consequently, to reach the initial goal of maintaining a $\lambda = 1$, further sterilisation campaigns should be conducted in the next few years, as it has not yet impacted the population as expected: the number of infants is still increasing from 2017 while it was expected to decrease. Yet, such a conclusion is perhaps hasty since sterilisations occurred recently. We might notice an impact of sterilisations in the next few years (although it is improbable in light of the projections and if the current resources conditions remain unchanged). An important remark about projections is that they do not consider any variability in the vital rates, i.e. the projection matrix coefficients, (except for sterilisation rate and epidemic outbreak parameters) which is not realistic. In fact, any population vital rates should vary through time according to the population dynamics, which are linked to the environmental conditions. Thus, one must be cautious while interpreting projections results.

The human primate interface is causing a problem around the world by endangering primate populations or by being the origin of their explosion (cf. Else (1991), Hockings et al. (2016), and Strum (1994, 2010)), which requires management solutions (Cowlishaw et al., 2000; Southwick et al., 1979). Among the non-lethal management plans to mitigate human-primate conflicts due to primate pests, the most documented is probably the one of Wong and Chow (2004), that was launched in 1999 and attempted to reduce the

exploding population of rhesus macaques in Hong Kong through sterilisation of both males and females. In addition to feeding ban (Fuentes, Gumert, et al., 2011), monkeys were sterilised via contraceptive/neutering and female tubectomy through campaigns that spread over more than 10 years (*Agriculture, Fisheries and Conservation Department: Contraceptive programme* 2010; Fuentes, Gumert, et al., 2011; Shek et al., 2010; Wong and Chow, 2004; Wong and Ni, 2000). As stated in the assessments over the years, the sterilisation program is a success since the population size has decreased from 2008 (Shek et al., 2010). These results suggest that sterilisation has direct impacts on population trends. Especially, since the population of macaques in Hong Kong is bigger than the one of Ubud, we could see a real influence of the program on the population trends in Ubud, if more efforts of sterilisation occur in the future (ideally along with a decrease of provisioning).

This master's thesis thus presents new possibilities for population management in the near future. The construction of the model from its more complete version to its final version offers a guideline on what could be done. The complete, reasonable or final model could thus potentially be reused in the future when data will be more robust and over a longer period of time (especially for the effect of rank on the reproductive success). This construction is however based on more or less subjective decisions that another person would perhaps make differently: other ways of simplifications and manipulations of the model could be considered. C parameter was included into the model as a constant, which is relevant although it would be ideal to estimate this parameter. In fact, the values inserted as constants are the overall mortality of each class for 2012. They are an estimation of the impact of the epidemic, but do not represent it realistically (mortality is not only due to the epidemic outbreak). Additionally, the sex ratio included in the equations of stages 4 and 6 was of $50 : 50$, which is perhaps not biologically justified as sex ratio at birth is 1:1 but not necessarily in later stages. However, it would be worth to estimate this ratio in SAS®. I personally did not try this manipulation because I realised the mistake too late, but it would be interesting to test it. It would also be interesting to conduct specific census in Ubud focusing on this question.

In perspective, new parameters related to the species/population biology could be contemplated to model the population in the future. For instance, the influence of the hierarchical status on the female reproductive success is supposed to be influenced by other factors as it seems to be a combined effect of rank, group density and/or habitat quality (food scarcity, provisioning) (van Noordwijk and van Schaik, 1999). It would thus be interesting to collect data on several groups (ideally all of them) of the study population to represent different conditions and compare their results. Then, we could potentially model the groups of the population rather than the entire population, because groups vary in density and each of them uses its own range of habitats which can vary in resources. This kind of model would represent the population more accurately. Moreover, we did not notice any difference in survival between fertile and sterile females, but we could imagine that sterilised females show a higher mortality than fertile females. In macaques giving birth and lactating offspring attracts other females' attention and enhances the social bonds and alliances, which participates in the animals' quality of life and thus survival (of both mother and infant) (Dunayer et al., 2018; Gumert, 2007; Silk, 1999; Silk et al., 2009). If sterilised females reveal to become progressively less connected and more peripheral within their group than fertile females (a hypothesis currently under test: Giraud et al. (in press)), we could perhaps notice a difference in survival between sterilised and fertile

females in the future and so consider both $S4s$ and $S4$. The fecundity of SF and AF were considered as one fecundity ($F5$), though in reality subadult and adult females should have distinctive fecundities. In fact, SF display high proceptive behaviours towards males due to hormonal changes (higher sexual motivation) but they are more prone to neo- or perinatal loss while AF are more experienced as mothers but are expected to see their birth rate decrease from a certain age (Anderson, 1986). It would therefore be preferable to distinguish birth rates between SF and AF. Also, the proximity to humans severely impacts the the life of the monkeys. More precisely, many deaths occur due to traffic and uncontrolled electric lines. These accidents are systematically recorded by the Monkey Forest staff. They could be considered as stochastic events for supplementary projections, to measure the direct impact of humans on the macaque population. Finally, if the scientific team members want to improve the population modelling in the next research projects, they could use an individual-based model instead of a population matrix model. The entity of such models are individuals considered as discrete organisms and characterised by a range of variables, phenology or behaviours. In this case, an individual-based model could be interesting since it considers a larger range of individual characteristics and their link with the biotic and abiotic factors, making the simulation more realistic (DeAngelis et al., 2014; Judson, 1994). For example, we could include parameters related to female reproductive success more easily (rank, age, experience, ...) or consider the migration patterns of the males, or their hierarchy.

CONCLUSION

Nowadays, many animal populations face HIREC pressures influencing their demographic trends and often threatening their survival (Isabirye-Basuta et al., 2008; Sih, Ferrari, et al., 2011; Sih, Trimmer, et al., 2016). In the tropics particularly primate populations cohabit with humans in human-primate interface, mainly due to habitat disturbances (Daspit, 2006; Estrada et al., 2017; Galán-Acedo et al., 2019; Sih, Ferrari, et al., 2011). In such conditions, either populations decline or they expand successfully (Daspit, 2006; Galán-Acedo et al., 2019; Robertson et al., 2013; Sih, Ferrari, et al., 2011). The application of PVA is predominant to predict how wild populations may adapt to remarkable demographic variations (Akçakaya et al., 2000; Beissinger et al., 1998; Boyce, 1992; Keedwell, 2004; Reed, Mills, et al., 2002; Reed, Murphy, et al., 1998). The population of the commensal long-tailed macaques of Ubud (Bali), with its low mortality and high fecundity rates (Brotcorne, Fuentes, et al., 2015; Cloutier et al., 2018), thrived in this overlapping area with humans, due to its impressive adaptability (Fuentes, 2010; Lane et al., 2010). It is characterised by overcrowding and requires an impactful population control for stabilising the population size, in order to reduce the conflicts with local people and mitigate the intense social tensions among primates. A sterilisation (females tubectomy) program thus started in 2017, and allowed to establish the number of females to sterilise on the basis of a matrix population model (Brotcorne, 2014, 2019; Cloutier et al., 2018).

Throughout this thesis, I attempted to refine the previous population matrix model by integrating the updated data collected between 2017 and 2020 and new parameters related to the female behaviour (rank and maternal experience). I based my work on and revised the model established by Cloutier et al. (2018) first theoretically and second through statistical analyses using SAS® software. The most simplified version, that is the one presenting the best cost effectiveness in fitting to the data quantified by setting most adequately its lowest *AICc* score, only considered the new sterilised females and the updated data. Behavioural parameters could not be included mainly due to a lack of consistency in the data sets. Projections over 25 years suggest that, if the current environmental conditions (i.e. excess of provisioning and lack of space) remain unchanged, the population will still increase in the future despite the efforts already initiated to stabilise the population. In conclusion, more efforts on population management by means of regular sterilisation campaigns should be undertaken in the future to mitigate population growth.

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Appendix A

Michelin female hierarchy and respective births and offspring survival

ID	Rank	DS	Category	Infants	fy	Survivors
Asym	1	12.877500	High-ranking	2	3	2
H11 Bosom	2	10.187900	High-ranking	1	3	1
H4 Nipples	3	7.827800	High-ranking	2	3	2
H3 Yeah	4	7.357200	High-ranking	2	3	2
Young	5	4.576500	High-ranking	2	2	2
Bat	6	4.484200	High-ranking	2	2	1
Black Tits	7	3.785000	High-ranking	2	3	2
Telinga	8	3.485600	High-ranking	2	3	2
Putih	9	3.265000	High-ranking	1	2	1
Snick	10	2.762900	High-ranking	2	3	1
Spotty	11	2.539000	High-ranking	1	3	0
Crunched	12	2.103200	High-ranking	1	3	0
You	13	1.664600	High-ranking	2	2	2
Tugas	14	1.658400	High-ranking	2	2	2
Cleft	15	1.275600	High-ranking	2	3	1
Excroissance	16	1.213800	High-ranking	2	2	2
H7 Lauren	17	0.844800	High-ranking	1	3	1
Tip	19	0.408100	High-ranking	1	3	1
Slash	20	-0.527100	High-ranking	3	3	3
Trivial	21	-0.562200	High-ranking	2	2	2
Hole	22	-0.647700	High-ranking	2	2	2
Bang	23	-0.799500	Low-ranking	2	2	1
H13 Torticoli	24	-1.093400	Low-ranking	2	3	1
White	25	-1.311100	Low-ranking	2	3	2

Stain	26	-1.351800	Low-ranking	0	1	NA
Trident	27	-1.688600	Low-ranking	3	3	3
Arcade	28	-1.747900	Low-ranking	2	3	2
Tuft	29	-1.891400	Low-ranking	2	3	2
H9 Tumeur	30	-2.002200	Low-ranking	2	3	2
H14 Pink	32	-2.891100	Low-ranking	2	2	1
Dua	33	-3.164000	Low-ranking	2	2	2
H1	34	-3.279400	Low-ranking	0	2	NA
Crack	35	-3.715700	Low-ranking	2	3	1
Helix	36	-3.818700	Low-ranking	2	2	1
H10 Mimi	37	-3.824700	Low-ranking	2	2	1
Snag	39	-4.465900	Low-ranking	1	2	1
H5 Pincang	41	-5.037500	Low-ranking	1	2	1
H6 Terkulai	42	-5.236100	Low-ranking	1	3	1
H8 Wink	43	-5.521200	Low-ranking	2	3	2
Gutter	44	-7.512100	Low-ranking	2	2	2

Table A.1: Results of the hierarchy and females individual histories. These results were used as data for the logistic regression to establish the relation between the rank and the birth rates/survival rates. From left to right: ID = names of the identified females, Rank = individual rank of the females in the hierarchy, DS = David Score values, Category = categories determined from the DS values, Infants = number of infants born to female, fy = number of years a female was observed, Survivors=number of infants that survived from birth to at least 8 months old.

Appendix B

Respective birth rates and offspring survival rates of AF and SF

Year	Subadult females					Adult females				
	SF	I	BR	S	SR	AF	I	BR	S	SR
2017	1	0	0	/	/	22	12	0.55	11	0.92
2018	6	0	0	/	/	46	31	0.67	27	0.87
2019	9	3	0.11	2	0.67	46	29	0.63	18	0.62
Means	5.33	1	0.33	2	0.67	38	24	0.62	18.67	0.8

Table B.1: Empirical results of the respective birth and offspring survival rates for subadult females and adult females of the Michelin group between 2017 and 2019, with respective means. From left to right: SF = number of subadult females, I = number of births, BR = birth rate, S = number of survivors from birth to at least 8 months old, SR = offspring survival rate from birth to at least 8 months old, AF = number of adult females.

Appendix C

Detailed procedure of modeling in SAS

I Implementing the reasonable model in SAS

Please find below the complete script in SAS (Section II).

The census data was first implemented in SAS and another data set was generated by SAS, where an observation corresponds to a couple of years (observed and predicted) including the observed abondance of each stage per year (Table C.1).

time	nobs1	nobs2	nobs36	nobs4	nobs4s	nobs5	nobs5s	nobs78	nobs9
2010	92	76	97	31	0	177	0	30	35
2011	90	91	118	37	0	197	0	39	44
2013	98	60	107	34	0	166	0	52	46
2014	100	86	108	32	0	218	0	50	65
2016	119	98	92	30	0	248	0	33	58
2017	119	118	167	29	0	201	16	34	63
2018	130	147	182	24	0	209	36	46	82
2019	169	189	203	19	12	211	90	82	82
2020	182	126	187	40	0	234	131	82	117

time_previous	n1_previous	n2_previous	n36_previous	n4_previous	n4s_previous	n5_previous	n5s_previous	n78_previous	n9_previous
2009	83	68	92	27	0	155	0	39	34
2010	92	76	97	31	0	177	0	30	35
2011	90	91	118	37	0	197	0	39	44
2013	98	60	107	34	0	166	0	52	46
2014	100	86	108	32	0	218	0	50	65
2016	119	98	92	30	0	248	0	33	58
2017	119	118	167	29	0	201	16	34	63
2018	130	147	182	24	0	209	36	46	82
2019	169	189	203	19	12	211	90	82	82

Table C.1: Couples of data generated by SAS® from the census data set collected between 2009 and 2020.

Then, I defined the fixed parameters values such as $RANK$, PF, $STERILSF$ and $STERILAF$. I forced the model to split stages 4 and 5 into 4A and 4B, and 5A and 5B with the parameter $RANK$ equal to 0.5, following the logic of the hierarchical data set. Similarly, population censuses of J2 (nobs36), SM (nobs78) and infants (nobs1) were split into stages 3 and 6, stages 7 and 8 and stages 1A and 1B, by introducing three $SPLIT$ parameters called $SPLIT36$, $SPLIT78$ and $SPLIT1AB$ respectively. The exact numbers of individuals of stages 3 and 6, 7 and 8, and 1A and 1B taken separately in the yearly census data are

unknown, it would thus not be accurate to halve these numbers with a fixed parameter. In fact, in the field we observe only the total number of Infants, J2 and SM, we do not know about the real distribution between infants A and B, J2 and J2', and SM and SM'. Thus, we aim at estimating the distribution between in each of these six classes rather than fix it arbitrarily. This is why *SPLIT* parameters will be estimated and not fixed to a specific value.

Constraints are imposed on the parameters to force the optimisation algorithm to keep parameters estimates in the space of value that are possible in reality: survival rates must be between 0 and 1 because they are probabilities and fecundities must be positive but without an upper boundary. An extra set of linear constrains is added ($F4A > F4B$ and $F5A > F5B$) because, as mentioned before, fertilities are supposed to be higher for high-ranking females than for low-ranking. Similarly, other constrains are: $SA1 > S1B$, $S4A > S4B$, $S5A > S5B$. Afterwards, all the equations defining the model and the objective function are written.

Moreover, some parameters were implemented with an initial starting value. Putting initial values helps the algorithm to converge, as it indicates "where to start". In other words, instead of starting to run from randomly assessed initial values the program will begin the estimations from an imposed value that is close to the reality (they are based on biological knowledge). This aid does not change the estimates since the algorithm will always rests on the data set.

II Script in SAS®

Here is the script of the *FULL MODEL*, that is the reasonable model, used as a start model for the estimation and simplifications step. The different comments are in green.

```
*Input census data;
*And generate data_output = couples of observed data per class and year;
data census;
 Infile datalines DLM='09'x dsd;
 input time nobs1 nobs2 nobs36 nobs4 nobs4s nobs5 nobs5s nobs78 nobs9;
 retain time_previous n1_previous n2_previous n36_previous n4_previous n4s_previous
n5_previous n5s_previous n78_previous n9_previous 0;
 merge=1;
 t+1;
 if t>1 then output;
 time_previous=time;
 n1_previous=nobs1;
 n2_previous=nobs2;
 n36_previous=nobs36;
 n4_previous=nobs4;
```

```
 n4s_previous=nobs4s;
 n5_previous=nobs5;
 n5s_previous=nobs5s;
 n78_previous=nobs78;
 n9_previous=nobs9;
 drop t;
    datalines;
    2009 83 68 92 27 0 155 0 39 34
    2010 92 76 97 31 0 177 0 30 35
    2011 90 91 118 37 0 197 0 39 44
    2013 98 60 107 34 0 166 0 52 46
    2014 100 86 108 32 0 218 0 50 65
    2016 119 98 92 30 0 248 0 33 58
    2017 119 118 167 29 0 201 16 34 63
    2018 130 147 182 24 0 209 36 46 82
    2019 169 189 203 19 12 211 90 82 82
    2020 182 126 187 40 0 234 131 82 117
    ;
run;

title1 "Estimate survival rates and fertility from census data";
proc nlp data=census out=data_for_estimation outest=optim_results outall  fdigits=12
         maxiter=100000 maxfunc=10000
/* In summary, to obtain appropriate standard errors for least squares estimates,
you can use the LSQ statement with any of the COV= options,
or you can use the MIN statement with COV=2; */
 cov=2 CLPARM=PL;

* Least squares estimation : min sum of squares of fct;
 min fct;
* List of parameters to estimate with starting values;
 parms  F4A=0.5, F4B=0.5, F5A=0.5, F5B=0.5,
 S1A, S1B, S2, S3, S4A, S4B, S4s = 0.96,
 S5A, S5B, S5s = 0.96, S6, S7, S8, S9, S10,
 C2=0.8, C3=0.8, C5=0.8, C9 = 0.8,
 SPLIT36=0.5, SPLIT78=0.5, SPLIT1AB=0.5;

*Constraint parameters between boundaries;
 bounds 0 <= C2 <= 1,  0 <= C3 <= 1,  0 <= C5 <= 1,  0 <= C9 <= 1,
  0 <= SPLIT36 <= 1, 0 <= SPLIT78 <= 1, 0 <= SPLIT1AB <= 1;
```

```
*List of equations and parameters describing the cycle graph;
* 1) Fixed parameters;
/*Probability to be a dominant female or to have a dominant mother*/
RANK = 0.5;
/*PF= Probability to be a female (0.5 because birth sex ratio and no other data)*/
PF=0.5;
dt=time-time_previous;

* 2) Data modifications, equations and parameters;
/* Separation J2 and adolescents*/
n3_previous = n36_previous*SPLIT36;
n6_previous = n36_previous*(1-SPLIT36);
n7_previous = n78_previous*(SPLIT78);
n8_previous = n78_previous*(1-SPLIT78);

/*Force model to put two parallel stages for infants :
with a dominant (A) and subordonate (B) mother*/
n1A_previous = n1_previous*SPLIT1AB;
n1B_previous = n1_previous*(1-SPLIT1AB);

/*Force model to put two parallel stages for subadult
and adult females : dominants (A) and subordonates (B)*/
n4A_previous = n4_previous*RANK;
n4B_previous = n4_previous*(1-RANK);
n5A_previous = n5_previous*RANK;
n5B_previous = n5_previous*(1-RANK);

* 3) Define transition probabilities;
* STAGES 1;
T4A1A = F4A ;
T4B1B = F4B ;
T5A1A = F5A ;
T5B1B = F5B ;
*Set boundaries and linear constraints;
bounds 0 <= F4A, 0 <= F4B, 0 <= F5A, 0 <= F5B;
lincon F4A - F4B > 0, F5A - F5B > 0;

* STAGE 2;
T1A=S1A;
```

```
T1B=S1B;
bounds 0 <= S1A <= 1, 0 <= S1B <= 1;
lincon S1A - S1B > 0;

*STAGE 3;
T2=S2;
bounds  0 <= S2 <= 1;

*STAGES 4;
/*STERILSF = annual steril rate for SF*/
if time < 2020 then STERILSF = 0;
if time = 2020 then STERILSF = 0.3871;
bounds 0 <= S3 <= 1;
/*Equations*/
 T3A = PF * S3 * RANK * (1-STERILSF);
 T3B = PF * S3 * (1-RANK) * (1-STERILSF);
 T3s = PF * S3 * STERILSF;

* STAGES 5;
 /*STERILAF = annual steril rate for AF*/
 if time < 2018 then STERILAF = 0;
 if time = 2018 then STERILAF = 0.07373;
 if time = 2019 then STERILAF = 0.08733;
 if time = 2020 then STERILAF = 0.2037;
 bounds 0 <= S4A <= 1, 0 <= S4B <= 1, 0 <= S4s <= 1,
 0 <= S5A <= 1, 0 <= S5B <= 1,  0 <= S5s <= 1;
 lincon S4A - S4B > 0, S5A - S5B > 0;
 /*Equations*/
    T4A = S4A * (1- STERILAF);
    T4B = S4B * (1- STERILAF);
    T4s = S4s;
    T5A = S5A * (1- STERILAF);
    T5B = S5B * (1- STERILAF);
    T5s = S5s;
    T4As = S4A * STERILAF;
    T4Bs = S4B * STERILAF;
    T5As = S5A * STERILAF;
    T5Bs = S5B * STERILAF;

*STAGE 6;
```

```
T6 = (1-PF) * S6;
bounds 0 <= S6 <= 1;

*STAGE 7;
T7 = S7;
bounds 0 <= S7 <= 1;

*STAGE 8;
  T8 = S8;
bounds 0 <= S8 <= 1;

* STAGE 9;
T9 = S9;
T10 = S10;
bounds 0 <= S9 <= 1, 0 <= S10 <= 1;

* 4) Equations of the respective stages with the transition probabilities;
if dt = 1 then do;
    n1A_pred = T4A1A * n4A_previous + T5A1A * n5A_previous;
    n1B_pred = T4B1B * n4B_previous + T5B1B * n5B_previous;
    n2_pred = T1A * n1A_previous + T1B * n1B_previous;
    n3_pred  = T2 * n2_previous;
    n4A_pred = T3A * n3_previous;
    n4B_pred = T3B * n3_previous;
    n4s_pred = T3s * n3_previous;
    n5A_pred = (T4A * n4A_previous) + (T5A * n5A_previous);
    n5B_pred = (T4B * n4B_previous) + (T5B * n5B_previous);
    n5s_pred = (T4s * n4s_previous) + (T5s * n5s_previous) +
        (T4As * n4A_previous) + (T4Bs * n4B_previous)
        + (T5As * n5A_previous) + (T5Bs * n5B_previous);
    n6_pred = T6 * n3_previous;
    n7_pred = T7 * n6_previous;
    n8_pred = T8 * n7_previous;
    n9_pred =(T9 * n8_previous) + (T10 * n9_previous);
end;

*Add intermediary data for the missing years (2013 and 2015);
if dt = 2 then do;
    n1A_int = T4A1A * n4A_previous + T5A1A * n5A_previous;
    n1B_int = T4B1B * n4B_previous + T5B1B * n5B_previous;
```

```
    n2_int = T1A * n1A_previous + T1B * n1B_previous;
    n3_int = T2 * n2_previous;
    n4A_int = T3A * n3_previous;
    n4B_int = T3B * n3_previous;
    n4s_int = T3s * n3_previous;
   n5A_int = (T4A * n4A_previous) + (T5A * n5A_previous);
   n5B_int = (T4B * n4B_previous) + (T5B * n5B_previous);
   n5s_int = (T4s * n4s_previous) + (T5s * n5s_previous)
   + (T4As * n4A_previous) + (T4Bs * n4B_previous)
   + (T5As * n5A_previous) + (T5Bs * n5B_previous);
    n6_int = T6 * n3_previous;
    n7_int = T7 * n6_previous;
    n8_int = T8 * n7_previous;
    n9_int =(T9 * n8_previous) + (T10 * n9_previous);
    n1A_pred = T4A1A * n4A_int + T5A1A * n5A_int;
    n1B_pred = T4B1B * n4B_int + T5B1B * n5B_int;
    n2_pred = T1A * n1A_int + T1B * N1B_int;
    n3_pred = T2 * n2_int;
    n4A_pred = T3A * n3_int;
    n4B_pred = T3B * n3_int;
    n4s_pred = T3s * n3_int;
    n5A_pred = (T4A * n4A_int) + (T5A * n5A_int);
    n5B_pred = (T4B * n4B_int) + (T5B * n5B_int);
    n5s_pred = (T4s * n4s_int) + (T5s * n5s_int)
    + (T4As * n4A_int) + (T4Bs * n4B_int)
    + (T5As * n5A_int) + (T5Bs * n5B_int);
    n6_pred = T6 * n3_int;
    n7_pred = T7 * n6_int;
    n8_pred = T8 * n7_int;
    n9_pred =(T9 * n8_int) + (T10 * n9_int);
end;

*Include C parameter for year 2012;
if time=2012 then do;
   n2_pred = ((T1A * n1A_previous) + (T1B * n1B_previous)) * C2;
   n3_pred = T2 * n2_previous * C3;
   n5A_pred = ((T4A * n4A_previous) + (T5A * n5A_previous)) * C5 ;
   n5B_pred = ((T4B * n4B_previous) + (T5B * n5B_previous)) * C5;
   n6_pred = (T6 * n3_previous) * C3 ;
   n9_pred = ((T9 * n8_previous) + (T10 * n9_previous)) * C9;
```

```
   end;

* 5) Regroup what was split;
n78_pred= n7_pred + n8_pred;
n36_pred= n3_pred + n6_pred;
n1_pred = n1A_pred + n1B_pred;
n4_pred = n4A_pred + n4B_pred;
n5_pred = n5A_pred + n5B_pred;

* 6) Specify we want to minimize the residual sum of squares (RSS);
 fct = (n1_pred-nobs1)**2 + (n2_pred-nobs2)**2
        + (n36_pred-nobs36)**2 + (n4_pred-nobs4)**2
        + (n4s_pred-nobs4s)**2 + (n5_pred-nobs5)**2
        + (n5s_pred-nobs5s)**2 + (n78_pred-nobs78)**2
        + (n9_pred-nobs9)**2;
run;
```

III Verification step: prevent from minimum local optimisation

Before starting the parameter estimations and model simplifications, the reasonable model implemented in SAS® was verified. The verification step consists in varying the parameters starting values through *(i)* no putting any starting value, *(ii)* setting aberrant starting values and *(iii)* setting realistic starting values, *(iv)* comparing the results. Setting initial values can be considered as an assistance for the parameter estimations, as it helps the algorithm to converge. Especially when a model is based on few data and contains many parameters to estimate. By comparing the results of the verification step, one can see whether the model gives approximately the same values for the parameters, which indicates that the program can run the model and establish good estimates.

Appendix D

Details of simplifications

The two paths of simplifications are presented in Table D.1.

I C parameter

The first results of C parameters were stuck to the initial value ($= 0.8$), which indicates a bad estimation by the procedure due to some unknown bias.

First, the reasonable model took into account 4 epidemic outbreak parameters ($C2$, $C3$, $C5$ and $C9$) as the epidemics impacted 4 stages of the model. Nonetheless, all the juveniles are counted as one class in the field. Even if in the reality, J1 and J2 may be impacted differently, there is no evidence in the data to support it. It is therefore reasonable to assume that there is no difference between $C2$ and $C3$ and simplify the model with $C2 = C3$. Then, we know that AMs were also affected by the epidemic although on a smaller scale (mortality rate of 2.1%) comparatively to the other classes. The impact of the epidemic on AM may therefore be invisible at the population scale. Therefore, rejecting $C9$ from the model should not have dramatic influence on the population model, which is confirmed by an improvement in the AIC score (Table D.1). Following the logic, we can generalize the C parameter for Js and AFs. We know that the epidemic affected the Js by reducing their survival of 13.5% and the AFs of 22%, which makes a difference of less than 10% between the two classes. Even if this difference is statistically significant (Brotcorne, 2014; Brotcorne, Fuentes, et al., 2015)), generalize $C3$ and $C5$ as C should not influence drastically the parameters estimations. Even after many simplifications of the model (as in the first procedure as in the second), C parameter was always stuck to the given initial value, indicating an estimation problem probably due to limited data. So as not to delete the C parameter from the model because of its importance for the survival rates estimations, I finally decided to fix values for the C parameters. These values are those of the mortality rates calculated by F. Brotcorne (previous paragraph). Therefore, by introducing constants to the equations of Js ($C3 = 0.865$), AF ($C5 = 0.78$) and AM ($C9 = 0.979$) for year 2012, I simplify the model while keeping the effect of the epidemic outbreak on the population and thus not over-estimate the survival

rates.

II Subadult males and juveniles survivals

Even though it is biologically reasonable to suppose that the survivals between young J2 and old J2, as well as SM and SM' are different, our data set does not allow to distinguish significantly these survivals. In fact, we only know the survival rates from J2 to SM (nobs36 to nobs78) and from SM to AM (nobs78 to nobs9), but not separately. By simplifying these survival rates ($S9 = S8$ and then $S7 = S6$), the AIC score was lower, indicating that these simplifications were better in term of goodness of fit.

III Adults survivals

$S5A$, $S5B$, $S5s$ and $S10$ were always estimated as equal to 1. Since the number of adults is systematically greater than the number of subadults, the program automatically considers that all subadults survived until the adult stage, leading to $S = 1$, which is demographically inaccurate. A way of correcting the bias is to consider that the survivals are equal between the subadults and the adults ($S5A = S4A$, $S5B = S4B$, $S5s = S4s$ and $S10 = S8$). And it is confirmed by the AIC score that improves with these simplifications. Note that this problem could be resolved with enough data: with greater data set, the algorithm may be able to distinguish the SF/SM going to AF/AM and the adults remaining adults.

IV Differences between the high- and low-ranking individuals

The infants' survival is supposed to vary according to the mothers' rank. Nevertheless, the exact number of infants coming from high- versus low-ranking females is unknown, due to field limitations. That is why I included the $SPLIT1AB$ parameter, which was estimated by the program. The algorithm was not able to estimate $S1A$, $S1B$ or $SPLIT1AB$ properly. $SPLIT1AB$ was always equal or almost equal to 1. Consequently, $S1A$ was overestimated and $S1B$ close to 0 (underestimated), which is quite logical. To solve this issue, I tried several combinations to simplify $S1$. First, I used the results from van Noordwijk and van Schaik, 1999 study as follows: $S1A = 0.84$ and $S1B = 0.76$

$$\Longrightarrow \frac{S1A}{S1B} = \frac{0.84}{0.76} \Longleftrightarrow S1A = 1.1 \times S1B$$

Which was directly inserted into the equations of the respective transition probabilities:

$$T1A = S1 \times 1.1$$

$$T1B = S1$$

Then, the model could never estimate properly the value of $SPLIT1AB$. Which is understandable because the data set does not explain a difference in infants' survivals. Indeed, the number of infants A and infants B is unknown. The only information the program has is the total number of infants and the number of J1. It will hence not be able to estimate a difference of survival. Regarding these difficulties, stages 1A and 1B were regrouped into one stage 1 in order to reduce the model's complexity.

Similarly, the data does not prove any difference in fecundities neither survivals for females. The results of van Noordwijk and van Schaik, 1999 indicate a difference in fertilities and survival only for top-reproductive females (8-20 years old), which corresponds to the AF stage. Nevertheless, as rank is stable over time, I found interesting to test whether there was a difference in fertilities or survival for both SF and AF. However, the modelling shows that it is more reasonable to regroup stages 4A and 4B into one stage 4 and have only one fertility ($F4A = F4B = F4$). It is important to highlight that differences in survival had to be considered from stage 4 anyway, since the survivals of stages 5 were simplified as equal to the survivals of stages 4 previously. However, an important question was whether there is a difference in survivals and/or fecundities between AF A and AF B. Several combinations were performed, where the last set of parameters to simplify was the fecundities regarding their importance in the sterilisation program. Therefore, from van Noordwijk and van Schaik, 1999 results, I established: $S4A = 0.58$ and $S4B = 0.42$

$$\Longrightarrow \frac{S4A}{S4B} = \frac{0.58}{0.42} \iff S4A = 1.38 \times S4B$$

Which was directly inserted into the equations of the respective transition probabilities:

$$T5A = S4 \times 1.38$$

$$T5B = S4$$

Following the same logic, fecundities were estimated as follows:

$$F5A = F5 \times 1.1$$

$$F5B = F5$$

Finally, $F4$ was simplified as equal to $F5$. $F4$ was always estimated to 0, likely due to the overestimation of $F5$. In fact, there are too many AF compared to the number of SF which insert bias into the estimation of $F4$. Because there was always bias generated, stages 5A and 5B were also regrouped into one stage 5, where no difference in survival nor fecundity was made.

(a) Procedure of simplification 1

Model	Model label	K	RSS	n	AIC	AICc
0	FULL = Reasonnable model	27	40559.80	81	557.503	586.031
1	0 + C2 = C3	26	40559.80	81	555.503	581.503
2	1 + no C9	25	40559.80	81	553.503	577.139
3	2 + C2 = C3 = C5 = C	24	40559.80	81	551.503	572.931
4	3 + S9 = S8	23	40867.41	81	550.115	569.483
5	4 + S7 = S6	22	40987.53	81	548.352	565.052
6	5 + S10 = S8	21	41007.13	81	546.391	562.052
7	6 + S5A=S4A, S5B=S4B,S5s=S4s	18	41561.480	81	541.479	552.511
8	7 + C3, C5	19	41561.480	81	543.479	555.938
9	7 + S1A=1.1× S1, S1B=S1	17	41000.750	81	538.379	548.093
10	7 + one stage 1	16	41561.480	81	537.479	545.979
11	10 + F4A=F4B=F4	15	41561.480	81	535.479	542.863
12	11 + one stage 4	15	41561.390	81	535.479	542.863
13	12 + S4A=S4× 1.38, S4B=S4	14	41835.930	81	534.012	540.376
14	13+ F5A=1.1× F5, F5B=F5	13	41903.170	81	532.142	537.575
15	14 + F4=F5	12	42868.280	81	531.986	536.575
16	15 + S4A=S4B=S4	12	42536.440	81	531.357	535.945
17	15 + one stage 5 (F5A=F5B=F5)	12	42584.500	81	531.449	536.037
18	17 + S4s=S4	11	42663.610	81	529.599	533.425
19	18 + C3 & C5 & C9 constants	10	42663.610	81	527.599	530.742

(b) Procedure of simplification 2

Model	Model label	K	RSS	n	AIC	AICc
0 bis	FULL = reasonnable model	27	40559.800	81	557.503	586.031
1 bis	0 bis + S9=S8	26	40957.230	81	556.293	582.293
2 bis	1 bis + S7=S6	25	40987.530	81	554.352	577.989
3 bis	2 bis + S4A=S4B=S4	24	40987.530	81	552.352	573.781
4 bis	3 bis + F4A=F4B=F4	23	40987.530	81	550.352	569.721
5 bis	4 bis + one stage 4	23	38324.170	81	544.910	564.279
6 bis	5 bis + S5A=S4A, S5B=S4B,S5s=S4s5s	21	38970.570	81	542.265	557.926
7 bis	6 bis + S4A=S4B=S4, S5s=S4s5s, S5A=S4× 1.38, S5B=S4	20	39080.600	81	540.494	554.494
8 bis	7 bis + S1A=1.1× S1, S1B=S1	19	41691.580	81	543.732	556.191
9 bis	7 bis + S1A=S1B=S1	19	41124.720	81	542.623	555.082
10 bis	9 bis + one stage 1, S5A=S4A=S5B=S4B=S4, S5s=S4s5s	18	41541.950	81	541.441	552.473
11 bis	10 bis + F5A=F5× 1.1,F5B=F5	17	41541.950	81	539.441	549.155
12 bis	11 bis + one stage 5 (F5A=F5B=F5)	17	41541.950	81	539.441	549.155
13 bis	12 bis + F4=F5	15	42565.810	81	537.413	544.798
14 bis	13 bis + C2=C3	15	42565.810	81	537.413	544.798
15 bis	14 bis + no C9	15	42565.810	81	537.413	544.798
16 bis	15 bis + S4s5s=S4	13	42644.950	81	533.563	538.996
17 bis	16 bis + C5=C3=C	12	42644.950	81	531.563	536.152
18 bis	17 bis + S10=S8	11	42663.610	81	529.599	533.425
19 bis	18 bis + C3 & C5 & C9 = constants	10	42663.610	81	527.599	530.742

Table D.1: Details of the two procedures of simplifications and model candidates tested with their respective AIC and AICc scores. K = number of parameters, RSS = residual sum of squares, the objective function to minimize, n = sample size.